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THEORY FOR THE DEVELOPMENT OF NEURON SELECTIVITY: ORIENTATION
SPECIFICITY AND BINOCULAR INTERACTION IN VISUAL CORTEX⁽¹⁾

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ABSTRACT

The development of stimulus selectivity in primary sensory cortex of higher vertebrates is considered in a general mathematical framework. A synaptic evolution scheme of a new kind is proposed in which incoming patterns rather than converging afferents compete. The change in the efficacy of a given synapse depends not only on instantaneous pre and postsynaptic activities but also on a slowly varying time-averaged value of the postsynaptic activity. Assuming an appropriate nonlinear form for this dependence, development of selectivity is obtained under quite general conditions on the sensory environment. One does not require nonlinearity of the neuron's integrative power nor does one need to assume any particular form for intracortical circuitry. This is first illustrated in simple cases, e.g. when the environment consists of only two different stimuli presented alternately in a random manner. The following formal statement then holds: the state of the system converges with probability 1 to points of maximum selectivity in the state space. We next consider the problem of early development of orientation selectivity and binocular interaction in primary visual cortex. Giving the environment an appropriate form, we obtain orientation tuning curves and ocular dominance comparable to what is observed in normally reared adult cats or monkeys. Simulations with binocular input and various types of normal or altered environments show good agreement with the relevant experimental data. Experiments are suggested that could further test our theory.

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I. INTRODUCTION

It has been known for some time that sensory neurons at practically all levels display various forms of stimulus selectivity. They may respond preferentially to a tone of a given frequency, a light spot of a given color, a light bar of a certain length, retinal disparity, orientation, etc... We might, therefore, regard stimulus selectivity as a general property of sensory neurons, and conjecture that the development of such selectivity obeys some general rule. Most attractive is the idea that some of the mechanisms by which selectivities develop in embryonic or early post natal life are sufficiently general to allow a unifying theoretical treatment.

In the present paper we attempt to construct such a mathematical theory of the development of stimulus selectivity in cortex. It is based on: 1) an elementary definition of a general index of selectivity, 2) stochastic differential equations proposed as a description of the evolution of the strengths of all synaptic junctions onto a given cortical neuron.

The ontogenetic development of the visual system, particularly of higher vertebrates, has been very extensively studied. Since the work of Hubel and Wiesel (1959, 1962) it has been known that almost all neurons in the primary visual cortex (area 17) of the normally reared adult cat are selective; they respond in a precise and sometimes highly tuned fashion to a variety of features--in particular to bars or edges of a given orientation and/or moving in a given direction through their receptive fields. Further work has shown that the response characteristics of these cortical cells strongly depend on the visual environment experienced by the animal during

a critical period extending roughly from the 3rd to the 15th week of postnatal life. (see for example Hubel and Wiesel, 1965; Blakemore and Van Sluyters, 1975; Buisseret and Imbert, 1976; Fregnac and Imbert, 1978; and Fregnac, 1979). Although these experiments show that visual experience plays a determining role in the development of selectivity the precise nature of this role is still a matter of controversy.

Applying our general ideas to the development of orientation selectivity and binocular interaction in area 17 of cat visual cortex, we obtain a theory based on a single mechanism of synaptic modification that accounts for the great variety of experimental results on monocular and binocular experience in normal and various altered visual environments. In addition we obtain some new predictions.

It is known that various algorithms related to Hebb's principle of synaptic learning (Hebb, 1949) can account for the formation of associative and distributed memories (see for example Marr, 1969; Brindley, 1969; Anderson, 1970 and 1972; Cooper, 1973; Kohonen, 1977). We therefore suggest that it may be the same fundamental mechanism, accessible to detailed experimental investigation in primary sensory areas of the nervous system which is also responsible for some of the higher forms of central nervous system organization.

In sections II-IV, our ideas are presented in general form, section V is devoted to the development of orientation selectivity primarily in a normal visual environment, whereas in section VI it is shown that our assumptions also account for normal or partial development of orientation selectivity and binocularity in various normal or altered visual environments.

II. PRELIMINARY REMARKS AND DEFINITIONS

Notation

We simplify the description of the dynamics of a neuron by choosing as variables not the instantaneous incoming time-sequence of spikes in each afferent fiber, the instantaneous membrane potential of the neuron or the time-sequence of outgoing spikes, but rather the pre and postsynaptic firing frequencies. These may be thought of as moving time-averages of the actual instantaneous variables³, where the length of the averaging interval is of the order of magnitude of the membrane time-constant τ . Throughout this paper, these firing frequencies are used as instantaneous variables. This formal neuron is thus a device which performs spatial integration (it integrates the signals impinging all over the soma and dendrites) rather than spatio-temporal integration: the output at time t is a function of the input and synaptic efficacies at t , independent of past history.

A synaptic efficacy m_i characterizes the net effect of presynaptic neuron i on the postsynaptic neuron (in most of the paper only one postsynaptic neuron is considered). This effect may be mediated through a complex system including perhaps several interneurons some of which are excitatory, other inhibitory. The resulting "ideal synapse" (Nass and Cooper, 1975) may thus be of either sign depending on whether the net effect is excitatory or inhibitory; it may also change sign during development.

A further simplification is to assume that the integrative power of the neuron is a linear function, that is:

$$c(t) = \sum_j m_j(t) d_j(t) \quad (1)$$

where $c(t)$ is the output at time t , $m_j(t)$ is the efficacy of the j -th synapse at time t , $d_j(t)$ is the j -th component of the input at time t (the firing frequency of the j -th presynaptic neuron) and \sum_j denotes summation over j , i.e., over all presynaptic neurons. We can then write:

$$\begin{aligned} m(t) &= (m_1(t), m_2(t), \dots, m_N(t)) \\ d(t) &= (d_1(t), d_2(t), \dots, d_N(t)) \\ c(t) &= m(t) \cdot d(t) \end{aligned} \quad (2)$$

$m(t)$ and $d(t)$ are real-valued vectors, of the same dimension, N , i.e., the number of ideal synapses onto the neuron, and $c(t)$ is the inner product (or "dot product") of $m(t)$ and $d(t)$. The vector $m(t)$, i.e. the array of synaptic efficacies at time t , is called the state of the neuron at time t . (Note that $c(t)$ as well as all components of $d(t)$ represent firing frequencies that are measured from the level of average spontaneous activity; thus they might take negative as well as positive values; $m_j(t)$ is dimensionless.)

The precise form of the integrative power is not essential: our results remain unchanged if for instance $c(t) = S(m(t) \cdot d(t))$ with S a positive-valued sigmoid-shaped function (see Bienenstock, 1980). This is in contrast to other work (e.g. Von der Malsburg, 1973) that does require nonlinear integrative power (see Appendix B).

Selectivity

It is common usage to estimate the orientation selectivity of a single visual cortical neuron by measuring the half-width at half-height--or an

equivalent quantity--of its orientation tuning curve. The selectivity is then measured with respect to a parameter of the stimulation, namely the orientation, which takes on values over an interval of 180° . In the present study, various kinds of inputs are considered, e. g. formal inputs with a parameter taking values on a finite set of points, rather than a continuous interval. It will then be useful to have a convenient general index of selectivity, defined in all cases. We propose the following:

$$\text{Sel}_{\mathcal{d}}(\mathcal{N}) = 1 - \frac{\text{mean response of } \mathcal{N} \text{ with respect to } \mathcal{d}}{\text{maximum response of } \mathcal{N} \text{ with respect to } \mathcal{d}}. \quad (3)$$

With this definition, selectivity is estimated with respect to, or in an environment for the neuron, that is, a random variable \mathcal{d} that takes on values in the space of inputs to the neuron \mathcal{N} . The variable \mathcal{d} represents a random input to the neuron, and is characterized by its probability distribution that may be discrete or continuous. (During normal development, the input to the neuron (or neuronal network) is presumably distributed uniformly over all orientations. In abnormal rearing conditions (e.g. dark reared) the input during development could be different from the input for measuring selectivity. How this should be translated in the formal space R^N will be discussed in section V). This distribution defines an environment, mathematically a random variable \mathcal{d} . Selectivity is estimated (before, or after development) with respect to this same environment⁴. Obviously, $\text{Sel}_{\mathcal{d}}(\mathcal{N})$ always falls between 0 and 1, and the higher the selectivity of \mathcal{N} in \mathcal{d} , the closer $\text{Sel}_{\mathcal{d}}(\mathcal{N})$ is to 1.

When applied to the formal neuron in state m definition (3) gives:

$$\text{Sel}_{\mathcal{Q}}(m) = 1 - \frac{E[m \cdot \mathcal{Q}]}{\text{ess sup}(m \cdot \mathcal{Q})}$$

where \mathcal{Q} is any R^N -valued random variable (the formal environment for the neuron). The symbol $E[\dots]$ stands for "expected value of ..." (i.e. mean value with respect to the distribution of \mathcal{Q}) and "ess sup of ..." (essential supremum) is equivalent to "maximum of ..." in most common applications. This is illustrated in Fig. 1.

III. MODIFICATION OF CORTICAL SYNAPSES

The various factors that influence synaptic modification may be divided broadly into two classes--those dependent on global and those dependent on local information. Global information in the form of chemical or electrical signalling presumably influences in the same way most (or all) modifiable junctions of a given type in a given area. Evidence for the existence of global factors that affect development may, for instance, be found in Kasamatsu and Pettigrew (1976, 1979), Singer (1979, 1980), and Buisseret et al. (1978). On the other hand, local information available at each modifiable synapse can influence each junction in a different manner. In this paper we are primarily interested in the effect of local information on the development of selectivity.

An early proposal as to how local information could affect synaptic modification was made by Hebb (1949). His, now classical, principle was suggested as a possible neurophysiological basis for operant conditioning: "when an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased". Thus the increase of the synaptic strength connecting A to B is dependent upon the correlated firing of A and B. Such a correlation principle has inspired the work of many theoreticians on various topics related to learning, associative memory, pattern recognition, organization of neural mappings (retinotopic projections) and development of selectivity of cortical neurons.

It is fairly clear that in order to actually use Hebb's principle one must

state conditions for synaptic decrease as specific as those for synaptic increase: if synapses are allowed only to increase, all synapses will eventually saturate; no information will be stored and no selectivity will develop (see for example Sejnowski, 1977a, b). What is required is thus a complementary statement to Hebb's principle giving conditions for synaptic decrease.⁵

Such statements usually have resulted in a form of synaptic competition. Consider, for example, one that was proposed by Stent (1973): "when the presynaptic axon of cell A repeatedly and persistently fails to excite the postsynaptic cell B while cell B is firing under the influence of other presynaptic axons, metabolic changes take place in one or both cells such that A's efficiency, as one of the cells firing B, is decreased". According to Stent's principle, the increase of the strength of certain synapses onto neuron B is accompanied by simultaneous decrease of the strength of other synapses onto the same neuron B. There thus occurs a spatial competition between convergent afferents. A competition mechanism of this kind provides a qualitative explanation of some experimental results on cortical development (e.g. monocularly deprived animals (Stent, 1973)) as well as some aspects of certain more complex deprivation paradigms such as those recently reported by Rauschecker and Singer (1981).

In the present work, we present a mechanism of synaptic modification that results in a temporal competition between input patterns rather than a spatial competition between different synapses. With this mechanism, whether synaptic strength increases or decreases depends upon the magnitude of the postsynaptic response as compared with a variable modification threshold. We show that this can account quantitatively in a more powerful way for increases and decreases in selectivity, as well as a great variety of other experimental results in diverse rearing conditions.

We propose that the change of the j -th synapse's strength at that time t obeys the following rule:

$$\dot{m}_j(t) = \phi(c_j(t))d_j(t) - \epsilon m_j(t) \quad (4)$$

where $\phi(c_j)$ is a scalar function of the postsynaptic activity, $c_j(t)$, that changes sign at a value, θ_M , of the output called the modification threshold:

$$\phi(c_j) < 0 \text{ for } c_j < \theta_M, \quad \phi(c_j) > 0 \text{ for } c_j > \theta_M$$

The term, $-\epsilon m(t)$, produces a uniform decay of all junctions; this in most cases does not affect the behavior of the system if ϵ is small enough. However, as will be seen later, it is important in some situations. Other than this uniform decay, the vector \underline{m} is driven in the direction of the input \underline{d} if the output is large (above θ_M) or opposite to the direction of the input if the output is small (below θ_M). As in hebbian modification, when $d_j > 0$ and c_j is large enough m_j increases. However, when $d_j > 0$ and c_j is not large enough, m_j decreases. We may regard this as a form of temporal competition between incoming patterns.

The idea of such a modification scheme was introduced in Cooper et al. (1979). Their use of a constant threshold θ_M , however, resulted in a certain lack of

robustness of the system: the response to all patterns could slip below Θ_M and then decrease to zero. In the absence of lateral inhibition between neurons, the response might increase to more than one pattern leading to stable states with maximal response to more than one pattern.

In this paper, we will see that making an appropriate choice for $\Theta_M(t)$ allows correct functioning under quite general conditions and provides remarkable noise-tolerance properties.

In our threshold modification scheme, the change of the j -th synapse's strength is written as a product of two terms, the presynaptic activity $d_j(t)$, and a function, $\phi(\zeta(t), \bar{\zeta}(t))$ of the postsynaptic variables, the output, $\zeta(t)$ and the average output $\bar{\zeta}(t)$. Making use of $\bar{\zeta}(t)$ in the evolutive power of the neuron is a new and essential feature of this work. It is necessary in order to allow both boundedness of the state and efficient threshold modification.

Neglecting the uniform decay term, for the moment, ($\epsilon=0$), in vector notation we have

$$\dot{w}(t) = \phi(\zeta(t), \bar{\zeta}(t)) d(t) \quad (5)$$

This, together with eq. 2, yields:

$$\dot{w}(t) = \phi(w(t) \cdot d(t), w(t) \cdot \bar{d}) d(t) \quad (6)$$

The crucial point in the choice of the function $\phi(c, \bar{c})$ is the determination of the threshold $\Theta_M(t)$, i.e., the value of c at which $\phi(c, \bar{c})$ changes sign. A candidate for $\Theta_M(t)$ is the average value of the postsynaptic firing rate, $\bar{\zeta}(t)$. The time average is meant to be taken over a period

T preceding t much longer than the membrane time-constant τ so that $\bar{c}(t)$ evolves on a much slower time-scale than $c(t)$. This can usually be approximated⁶ by averaging over the distribution of inputs for a given state $m(t)$

$$\bar{c}(t) = m(t) \cdot \bar{d}$$

This results in an essential feature, the instability of low selectivity points, as will now be informally shown.

As a simplification, assume that d takes on K discrete values d^1, \dots, d^K with equal probability and let m_0 be a low-selectivity equilibrium point.

Equilibrium means that the average $E[\phi(m_0 \cdot d)] = (1/K) \sum_{i=1}^K \phi(m_0 \cdot d^i) d^i$ is the null vector, while low-selectivity means that for most of the d^i 's, say all of them, the output $m_0 \cdot d^i$ is positive, and $m_0 \cdot d^i \approx m_0 \cdot d^j$ for all i and j . It follows that for all i ,

$$m_0 \cdot d^i \approx E[m_0 \cdot d] \approx \Theta_M(m_0) \text{ hence } \phi(m_0 \cdot d^i) \approx 0.$$

Consider now a small perturbation from equilibrium: $m = m_0 + x$. It is likely that x will "favor" some of the d^i 's to the detriment of others: a favored input is a d^i roughly pointing in the direction of x , which therefore satisfies $m \cdot d^i > \Theta_M(m)$, hence $\phi(m \cdot d^i) > 0$, while for the d^i 's directed opposite to x one has $\phi(m \cdot d^i) < 0$. Thus, when a favored input d^i comes in, the state m moves in its direction (eq. 6 with $\phi(c) > 0$), while when a

non-favored input comes in, it moves in the opposite direction. In summary, whatever the input d^1 , the state moves in the direction of the initial perturbation x , away from m_0 , which is therefore an unstable equilibrium point.

We may now state that if stable equilibrium points exist in the state space, they are of high selectivity. However do such points exist at all? The answer is generally yes provided that the state is bounded from the origin and from infinity. These conditions, instability of low-selectivity equilibria as well as boundedness, are fulfilled by a single function $\phi(c, \bar{c})$ if we define $\theta_M(t)$ to behave as a nonlinear function of $c(t)$, for example a power. The exponent should then be larger than 1. The final requirement on $\phi(c, \bar{c})$ thus reads:

$$\text{sign } \phi(c, \bar{c}) = \text{sign} \left(c - \left(\frac{\bar{c}}{c_0} \right)^p \bar{c} \right) \quad \text{for } c > 0 \quad (7)$$

$$\phi(0, \bar{c}) = 0 \text{ for all } \bar{c}$$

where c_0 and p are two fixed positive constants.⁷ The threshold $\theta_M(\bar{c}) = (\bar{c}/c_0)^p \bar{c}$ thus serves two purposes: allowing threshold modification when $\bar{c} \approx c_0$ as well as driving the state from regions such that $\bar{c} \ll c_0$ or $\bar{c} \gg c_0$. Equation (7) is illustrated in Fig. 2. The process of synaptic growth, starting near 0 to eventually end in a stable selective state, may be described as follows. Initially, $\bar{c} \ll c_0$ hence

$\phi(c, \bar{c}) > 0$ for all inputs in the environment: the responses to all inputs grow. With this growth \bar{c} increases, thus increasing θ_M . Now some inputs result in postsynaptic responses that exceed θ_M , while others--those whose direction is far away (close to orthogonal) from the favored inputs--give a response less than θ_M . The response to the former continues to grow while the response to the latter decays. This results in a form of competition between incoming patterns rather than competition between synapses. The response to unfavored patterns decays until it reaches 0, where it stabilizes, for $\phi(0, \bar{c}) = 0$ for any \bar{c} (equation 7). The response to favored patterns grows until the mean response \bar{c} is high enough, and the state stabilizes. This occurs in spite of the fact that many complicated geometrical relationships may exist between different patterns, i.e. that they are not orthogonal since different patterns may and certainly do share common synapses.

It should be stressed that this is only one solution among many possible others. The purpose of these equations is to provide a scheme (rather than a unique differential equation) that is biologically feasible, yet defined well enough for mathematical and numerical analysis. Considerable freedom is left in the exact choice of the function ϕ since p and c_0 may be almost arbitrarily chosen and, once this is done, the only requirements are on the sign of ϕ .

IV. MATHEMATICAL RESULTS

The behavior of system (6) depends critically on the environment, that is, on the distribution of the stationary stochastic process d . Two classes of distributions may be considered:

- discrete distributions: K possible inputs d^1, \dots, d^K .

These will generally be assumed to occur with the same probability $1/K$.

The process d is then a jump process which randomly assumes new values at each time increment. The vector m is (roughly) a Markov process.

- continuous distributions: in the present work, the only continuous distribution that will be considered is a uniform distribution d over a closed 1-parameter curve in the input space R^N (section V).

Although the principles underlying the convergence to selective states are intuitively fairly simple (see preceding section), mathematical analysis of the system is not entirely straightforward, even for the simplest d . Mathematical results, obtained only for certain discrete distributions, are of two types: 1) equilibrium points are locally stable if and only if they are of highest available selectivity with respect to the given distribution of d , 2) given any initial value of m in the state space, the probability that $m(t)$ converges to one of the maximum selectivity fixed points as t goes to infinity is 1. Results of the second type are much stronger, and require a tedious geometrical analysis. Results are stated here in a somewhat simplified form (obvious requirements of a very mathematical character are omitted). For exact statements and proofs, the reader is referred to Bienenstock (1980).

We first study the simple case where d takes on values of only two possible

input vectors d^1 and d^2 , that occur with the same probability:

$$P[d = d^1] = P[d = d^2] = 1/2.$$

Whatever the real dimension N of the system it reduces to two dimensions. (Any component of m outside the linear subspace spanned by d^1 and d^2 will eventually decay to 0 due to the uniform decay term.)

It follows immediately from the definition that the maximum value of $Sel_d(m)$ in the state space is $1/2$. It is reached for states m which give null response when d^1 comes in (i.e. are orthogonal to d^1) but positive response for d^2 -- or vice versa. Minimum selectivity, namely 0, is obtained for states m such that $m \cdot d^1 = m \cdot d^2$. Equilibrium states of both kinds indeed exist:

Lemma 1: Let d^1 and d^2 be linearly independent and d satisfy $P[d = d^1] = P[d = d^2] = 1/2$. Then for any ϕ satisfying eq. (7), eq. (6) admits exactly 4 fixed points, m^0 , m^1 , m^2 and $m^{1,2}$ with: $Sel_d(m^0) = Sel_d(m^{1,2}) = 0$, and $Sel_d(m^1) = Sel_d(m^2) = 1/2$. (Here the superscripts indicate which of the d^i are not orthogonal to m . (m^0 is the origin). Thus for instance $m^1 \cdot d^1 > 0$, $m^1 \cdot d^2 = 0$.)

The behavior of eq. 6 depends on the geometry of the inputs, in the present case on $\cos(d^1, d^2)$. The crucial assumption that is needed here is that $\cos(d^1, d^2) \geq 0$. This is a reasonable assumption which is obviously satisfied if all components of the inputs are positive, as is assumed in some models (Von der Malsburg, 1973; Perez et al., 1975). We may then state the following:

Theorem 1. Assume that in addition to the conditions of Lemma 1, $\cos(d^1, d^2) > 0$. Then m^0 and $m^{1,2}$ are unstable, m^1 and m^2 are stable, and whatever its initial value, the state of the system converges almost surely (i.e., with probability 1)

either to m^1 or to m^2 .

Theorem 1 is the basic result in the 2-dimensional setting: it characterizes evolution schemes based on competition between patterns, saying that the state eventually reaches maximal selectivity even when the two input vectors are very close to one another. Obviously this requires that some of the synaptic strengths be negative since the neuron has linear integrative power. Inhibitory connections are thus necessary to obtain selectivity (see also section V below). Some selectivity is also realizable with no inhibitory connections--not even "intracortical" ones--if the integrative power is appropriately nonlinear. However, whatever the nonlinearity of the integrative power, theorem 1 could not hold for evolution equations based on competition between converging afferents (see Appendix B).

In theorem 1, we have a discrete sensory environment which consists of exactly two different stimuli--a situation, although simple mathematically, not often encountered in nature. It may however, very well correspond to a visual environment restricted to only horizontally and vertically oriented contours, present with equal probability. Theorem 1 then predicts that cortical cells will develop a selective response to one of the two orientations, with no preference for either (other than what may result from initial connectivity). Thus, on a large sample of cortical cells, one should expect as many cells tuned to the horizontal orientation as to the vertical one. (So far, no assumption is made on intracortical circuitry. See Appendix D).

The proof of theorem 1 is based on the existence of trap regions around each of the selective fixed points:

Theorem 2: Under the same conditions as in Theorem 1, there exists around $m^1(m^2)$ a region $F^1(F^2)$ such that once the state enters $F^1(F^2)$, it converges almost surely to $m^1(m^2)$.

The meaning of theorem 2 is the following: once $m(t)$ has reached a certain selectivity; it cannot "switch" to another selective region. Applied to cortical cells in a patterned visual environment, this means that once they become sufficiently committed to certain orientations, they will remain committed to those orientations, (provided that the visual environment does not change), becoming more selective as they stabilize to some maximal selectivity'. Theorems 1 and 2 are illustrated in Figure 3.

It is worth mentioning that when $\cos(d^1, d^2) < 0$, the situation is much more complicated: trap regions don't necessarily exist and periodic asymptotic behavior, i.e., limit cycles, may occur, bifurcating from the stable fixed points when $\cos(d^1, d^2)$ becomes too negative (see Bienenstock, 1980).

We now turn to the case where d takes on K values. The following is easily obtained:

Lemma 2: let d^1, d^2, \dots, d^K be linearly independent and d satisfy $P[d = d^1] = \dots = P[d = d^K] = 1/K$. Then, for any ϕ satisfying equation (7), eq. (6) admits exactly 2^K fixed points with selectivities $0, 1/K, 2/K, \dots, (K-1)/K$. There are K fixed points m^1, \dots, m^K of selectivity $(K-1)/K$.

Obviously, $(K-1)/K$ is also the maximum possible selectivity with respect to d . It means a positive response for one and only one of the inputs. The

situation is now much more complicated than what it was with only 2 inputs: it is not obvious whether in all cases assuming that all the cosines between inputs are positive is sufficient to yield stability of the maximum selectivity fixed points. However, we may state the following:

Theorem 3: Assume, in addition to the conditions of Lemma 2, that d^1, \dots, d^K are all mutually orthogonal or close to orthogonal. Then the K fixed points of maximum selectivity are stable, and, whatever its initial value, the state of the system converges almost surely to one of them.

The proof of theorem 3 also involves trap regions around the K maximally selective fixed points, and the analog of theorem 2 is true here.

Although the general case has not yet been solved analytically, as will be seen in the next section, computer simulations suggest that for a fairly broad range of environments if $d^i \cdot d^j \geq 0$, even if d^1, \dots, d^K are far from being mutually orthogonal, the K fixed points of maximum selectivity are stable.

Simulations suggest further (see for instance Fig. 4b) that even if the d^1, \dots, d^K are not linearly independent and are very far from being mutually orthogonal, the asymptotic selectivity is close to its maximum value with respect to d .

V. ORIENTATION SELECTIVITY AND BINOCULAR INTERACTION IN VISUAL CORTEX

We now apply what has been done above to a concrete example, orientation selectivity and binocular interaction in primary visual cortex. The ordinary development of these properties in mammals depends to a large extent on normal functioning of the visual system (i.e. normal visual experience) during the first few weeks or months of post-natal life. This has been demonstrated many times by various experiments, based mainly on the paradigm of rearing the animal in a restricted sensory environment. In the next two sections, it is shown how equations (4)-(7) account for both normal development as well as development in restricted visual environments.

Consider first a classical test-environment used to construct the tuning curve of cortical neurons. This environment consists of an elongated light bar successively presented or moved in all orientations -- preferably in a random sequence -- in the neuron's receptive field. Thus all the parameters of the stimulus are constant except one, the orientation, which is uniformly distributed on a circularly symmetric closed path. We assume that the retino-cortical pathways maps this family of stimuli to the cortical neuron's space of inputs in such a way as to preserve the circular symmetry (as defined below). Thus, the typical theoretical environment that will be used for constructing the formal neuron's tuning curve is a random variable ϕ uniformly distributed on a circularly symmetric closed one-parameter family of points in the space R^N . The parameter coding orientation in the receptive field is, in principle, continuous. However, for the purpose of numerical simulations, the distribution is made discrete. Thus ϕ takes on values on the points d^1, \dots, d^K . The requirement of circular symmetry is expressed mathematically as follows:

the matrix of inner products of the vectors d^1, \dots, d^K is circular (i.e., each row is obtained from its nearest upper neighbor by shifting it one column to the right) and the rows of the matrix are unimodal. A random variable, d , uniformly distributed on such a set of points will be, hereafter, called a circular environment. Such a d may be roughly characterized by 3 parameters: N , K and a measure of the mutual geometrical closeness of the d^i 's, for instance $\min \cos(d^1, d^i)$.

We are now faced with the difficult problem of specifying the stationary stochastic process that represents the time-sequence of inputs to the neuron during development. In a first analysis, there is no choice but oversimplifying the problem by giving the stochastic process exactly the same distribution as the circular d defined above. In doing so, we assume that development of orientation selectivity is to a large extent independent of other parameters of the stimulus, e.g., contrast, shape, position in the receptive field, retinal disparity for binocular neurons, etc. The elementary stimulus for a cortical neuron is a rectilinear contrast edge or bar. Any additional pattern present at the same time in the receptive field is regarded as random noise. (A discussion of this point is given in Cooper et al. (1979)).

Va. NORMAL MONOCULAR INPUT

The behavior of a monocular system in circular environments is investigated by numerically simulating equation 6 with a variety of circular d 's and functions ϕ satisfying equation 7. In the simulations presented here, the dimensions of the input and state space is generally $N = 37$; the number K of input vectors varies from 12 to 60. (Various kinds of functions ϕ were used: some were

stepwise constant, others smooth, bounded or unbounded.) One may reasonably expect the system's behavior to be fairly independent of N and K if these are high enough. However, the geometry of \mathcal{d} may be determining: if the d^i 's are closely packed together in the state space, i.e., if $\min \cos(d^1, d^i)$ is close to 1, convergence to selective states may presumably be difficult to achieve or even impossible.

Simulations show the following behavior:

1. The state converges rapidly to a fixed point, or attractor.
2. Various such attractors exist. For a given \mathcal{d} and ϕ they all have the same selectivity, which is close to its maximum value in \mathcal{d} .
3. The asymptotic tuning curve is always unimodal. One may thus talk of the preferred orientation of an attractor.
4. There exists an attractor in each possible orientation.
5. If there is no initial preference, all orientations have equal probability of attracting the state. (Which one will become favored depends on the exact sequence of inputs). This does not hold for environments which are not perfectly circular, at least for a single neuron system as the one studied here.

Figs. 4a and 4b show respectively the progressive buildup of selectivity and the tuning curve when the state has virtually stabilized.

In summary then, the system behaves in circular environments exactly as we might have expected from the results of the preceding section. One should however note one important difference: the maximum selectivity for a continuous environment cannot be as simply calculated as it was before. It is only when d is uniformly distributed on K linearly independent vectors that we know that $\max_{d} \text{Sel}_d(m) = \frac{K-1}{K}$ (Lemma 2). Theorem 3 tells us that if in addition the vectors are nearly orthogonal to one another, this selectivity is indeed asymptotically reached. We could not prove that this is also true when the vectors are circularly arranged but not mutually orthogonal. However, it could not be disproved by any numerical simulation, so we conjecture that is indeed true. (Reasonable selectivity is attained even in most unfavorable environments. As an example, in a circular d such that all cosines fall between .94 and 1, a selectivity of .68 was reached after 12,000 iterations.) Notice that in the present context this question is only of theoretical interest, since naturally occurring environments are continuous rather than discrete. The behavior of our system in such an environment is very well approximated by a discrete circular d , provided that K is large enough. K is then presumably larger than N , the K inputs are linearly dependent and we have no explicit formula for $\max_{d} \text{Sel}_d(m)$.

The system thus functions well in a large class of environments. It should be stressed that the numerical value of the only parameter that appears

explicitly in the evolution scheme itself, namely the exponent p , is not at all critical. Simulations performed with a constant d , p being varied from .01 to 10, yield the same asymptotic limit for the selectivity; the height of the asymptotic tuning curve, i.e., $\max(m.d)$, is however highly dependent on p . This invariance property validates in a sense the definition of $\text{Sel}_d(x)$.

Inhibitory synapses are essential here exactly as they are in the 2-dimensional case. One way to show this is to substitute 0 for all negative components in the state once it has reached selectivity. This typically results in a drastic drop of selectivity (e.g. from .81 to .55) although a slight preference generally remains for the same orientation as before. This may be related to the experimental fact that local pharmacological deactivation of inhibitory connections strongly impairs orientation selectivity by rendering all orientations effective in triggering the cell's response (Sillito, 1975).

Finally, it should be mentioned that the system displays a good noise-tolerance, particularly when the state has already reached a selective region. The system then resists presynaptic additive noise with a signal-to-noise ratio of the order of 1, and postsynaptic noise with a signal-to-noise ratio as small as 1/4.

Vb. RESTRICTED MONOCULAR INPUT

To discuss this situation we must now include the exponential decay term, $-\epsilon p(t)$, previously neglected (Eq. 4). It is clear that the results stated above will be preserved if ϵ is sufficiently smaller than the average of

$|\phi(c, \bar{c})|$ (i.e., competition mechanisms are faster than decay). However, exponential decay may become crucial if one asks what is the response of the cell to patterns that were not represented in the environment during development.

Consider for instance an environment consisting of a single stimulus d^1 . It is then easily shown that system 6-7 admits one attractor m^1 that satisfies $m^1 \cdot d^1 \approx c_0$ for small ϵ ($m^1 \cdot d^1 = c_0$ for $\epsilon = 0$). Obviously, for $\epsilon > 0$, m^1 will satisfy $m^1 \cdot d = 0$ for any d orthogonal to d^1 . However the response to a pattern d not orthogonal to d^1 will depend both on ϵ and on $\cos(d, d^1)$. One may for instance find that $m^1 \cdot d \approx 1/2 (m^1 \cdot d^1)$ for $\cos(d, d^1) = .5$. If one computes now the selectivity of the neuron in state m^1 with respect to a circular environment (d^1, \dots, d^K) such that $\min \cos(d^1, d^i) = .5$, one will obviously get a low value, in fact $\text{Sel}_d(m^1) < .5$.

The one-stimulus environment may be regarded as a case corresponding to rearing the animal in a visual world where only one orientation is present. No controversy remains at present that rearing in such a visual environment results in a cortex in which all visually responsive cells are tuned to the experienced (or nearby) orientations (Blakemore and Cooper, 1970; Hirsch and Spinelli, 1970; 1971; see also Stryker et al., 1978). We see that our theory is in agreement with these findings; moreover we predict that in such a cortex the average selectivity of these cells should be lower than normal. Although there is so far no detailed quantitative study on this point in a recent work there is some indication that this may indeed be true: "more neurons with normal orientation tuning were found in the kittens that could see all orientations, or at least horizontal and vertical, than in the kittens that had experienced only one orientation" (Rauschecker and Singer, 1980).

Vc. BINOCULAR INPUT

We now consider a binocularly driven cell. The firing rate of the neuron at time t becomes

$$c(t) = m_r(t) \cdot d_r(t) + m_l(t) \cdot d_l(t) \quad (8)$$

with evolution schemes for "right" and "left" states m_r and m_l straightforward generalizations of eq. (4). Various possibilities now exist for the input (d_r, d_l) : one may wish to simulate normal rearing (both d_r and d_l circular and presumably highly correlated), monocular deprivation, binocular deprivation etc...

Detailed discussion of the results of simulations under various conditions is given in the next section. The main results are summarized here:

1. In a normal binocular environment, the cell becomes orientation selective, binocular, preferring the same orientation through both eyes.
2. In an environment simulating monocular deprivation, the cell becomes monocular and orientation-selective, whatever its initial state.
3. In environments simulating binocular deprivation, the cell does not lose its responsiveness, but does lose its orientation selectivity if it was present.

VI. DEVELOPMENT UNDER DIFFERENT REARING CONDITIONS

a) Related experimental data

This brief summary is restricted to area 17 of kitten's cortex. Most kittens first open their eyes at the end of the first week after birth. It is not easy to assess whether or not orientation selective cells exist at that time in striate cortex: few cells are visually responsive, and the response's main characteristics are generally "sluggishness" and fatigability. However, it is quite generally agreed that as soon as cortical cells are reliably visually stimulated (e.g. at 2 weeks), some are orientation selective, whatever the previous visual experience of the animal (cf. Hubel and Wiesel, 1963; Blakemore and Van Sluyters, 1975; Buisseret and Imbert, 1976; Frégnac and Imbert, 1978).

Orientation selectivity develops and extends to all visual cells in area 17 if the animal is reared, and behaves freely, in a normal visual environment (NR): complete "specification" and normal binocularity (about 80% of responsive cells) are reached at about 6 weeks of age (Frégnac and Imbert, 1978). However, if the animal is reared in total darkness from birth to the age of 6 weeks (DR), none or few orientation selective cells are then recorded (from 0 to 15%, depending on the authors and the classification criteria); however the distribution of ocular dominance seems unaffected (Blakemore and Mitchell, 1973; Imbert and Buisseret, 1975; Blakemore and Van Sluyters, 1975; Buisseret and Imbert, 1976; Leventhal and Hirsch, 1980; Frégnac and Imbert, 1978). In animals whose eyelids have been sutured at birth, and which are thus binocularly deprived of pattern vision (BD), a somewhat higher proportion (from 12 to 50% of the visually excitable cells are still orientation selective at 6 weeks (and even beyond 24 months of age) and the proportion of binocular cells is less than normal (Wiesel and

Hubel, 1965; Blakemore and Van Sluyters, 1975; Kratz and Spear, 1976; Leventhal and Hirsch, 1977, Watkins et al., 1978).

Of all visual deprivation paradigms, putting one eye in a competitive advantage over the other has probably the most striking consequences: monocular lid-suture (MD), if it is performed during a "critical" period (ranging from about 3 weeks to about 12 weeks), results in a rapid loss of binocularity, to the profit of the open eye (Wiesel and Hubel, 1963, 1965); then opening the closed eye and closing the experienced one may result in a complete reversal of ocular dominance (Blakemore and Van Sluyters, 1974). A disruption of binocularity that does not favor one of the eyes may be obtained, for example, by provoking an artificial strabismus (Hubel and Wiesel, 1965) or by an alternating monocular occlusion, which gives both eyes an equal amount of visual stimulation (Blakemore, 1976). In what follows, we call this uncorrelated rearing (UR).

b) Simulations

The aim of this section is to show that the experimental results briefly reviewed above follow from our assumptions if one chooses the appropriate distribution for d . The model system now consists in a single binocular neuron. The firing rate of the neuron at time t is given by

$$c(t) = m_r(t) \cdot d_r(t) + m_l(t) \cdot d_l(t) \quad (8)$$

where the indices r and l refer to right and left eye respectively. m_r (resp. m_l) obeys the evolution scheme described by equations 4-6, where d_r (resp. d_l) is substituted for d . The two equations are of course coupled, since $c(t)$ depends at each t on both $m_r(t)$ and $m_l(t)$.

The vector (d_r, d_l) is a stationary stochastic process, whose distribution is one of the following, depending on the experimental situation one wishes to simulate:

Normal Rearing (NR):

$d_r(t) = d_l(t)$ for all t , and d_r is circular. (Noise terms that may be added to the inputs may or may not be stochastically independent).

Uncorrelated Rearing (UR):

d_r and d_l are i.i.d. (independent identically distributed): they have the same circular distribution, but no statistical relationship exists between them.

Binocular Deprivation:

1. Total light deprivation (DR). The $2n$ components of (d_r, d_l) are i.i.d.: d_r and d_l are uncorrelated noise terms.
2. Binocular pattern deprivation (BD). $d_r(t) = \lambda_r(t)e$, $d_l(t) = \lambda_l(t)e$ where e is an arbitrary fixed vector with positive components, and λ_r and λ_l are scalar positive-valued i.i.d.

Monocular Deprivation (MD):

d_r is circular, d_l is a noise term: $d_l = n$

In the NR case, the inputs from the two eyes to a binocular cell are probably well correlated. We therefore assume that they are equal, which is mathematically equivalent. The DR distribution represents dark discharge. The BD distribution deserves a more detailed explanation. In this

distribution it is only the length λ_r and λ_l of the vectors \hat{d}_r and \hat{d}_l that varies in time. This length is thought to correspond to the intensity of light coming through each closed eyelid, whereas the direction of the vector in the input space is determined by the constant "unpatterned" vector e , e.g., $e = (1, 1, \dots, 1)$. One may indeed assume that when light falls on the retina through the closed lids, there is at any instant of time high correlation between firing rates of all retinal ganglion cells on a relatively large region of the retina. Inputs from the two eyes, however, are probably to some extent asynchronous (cf. Kratz and Spear, 1976); hence the BD distribution.

Simulations of the behavior of the system in these different environments give the following:

NR (Fig. 5a): all asymptotic states are selective, binocular with matching preferred orientations for stimulation through each eye.

DR (Fig. 5b): the motion of the state (\hat{m}_r, \hat{m}_l) resembles a random walk. (The small exponential decay term is necessary here too, in order to prevent large fluctuations). The two tuning curves⁸ therefore undergo random fluctuations, that are essentially determined by the second-order statistics of the input \hat{d} . As can be seen from the figure, these fluctuations may sometimes result in a weak orientation

preference or unbalanced ocular dominance. However, the system never stays in such states very long; its average state on the long run is perfectly binocular and non-oriented. Moreover, whatever the second-order statistics of d and the circular environment in which tuning curves are assessed, a regular unimodal orientation tuning curve is rarely observed, and selectivity never exceeds .6. We may thus conclude that orientation selectivity as observed in the NR case (both experimental and theoretical) cannot be obtained from purely random synaptic weights. It is worth mentioning here that prolonged dark rearing has been reported to increase response variability (Leventhal and Hirsch, 1980); a similar observation was made by Frégnac and Bienenstock (1981)⁹.

BD (Fig. 5c): Unlike the DR case, the state converges (as may easily be proved mathematically). Although there exist both monocular and binocular stable equilibrium points, the asymptotic state is generally monocular if the initial state is taken as 0. The orientation tuning curve is then

essentially determined by the relative geometry of the fixed arbitrary vector e and the arbitrary circular environment which serves to assess the tuning curve. Fine unimodal tuning is therefore not to be expected.

MD(Fig. 5d): The only stable equilibrium points are monocular and selective. The system converges to such states whatever the initial conditions. In particular, this accounts for reverse suture experiments (Blakemore and Van Sluyters, 1974; Movshon, 1976).

UR(Fig. 5e): This situation is in a sense similar to the BD one: the state converges, but monocular as well as binocular equilibria exist. As in the BD case, the asymptotic state generally observed with $m_r(0) = m_l(0) = 0$ is monocular. (This should be attributed to the mismatched inputs from the two eyes, as is done by most authors). In this case, however, asymptotic states are selective, and when they are binocular, preferred orientations through each eye don't necessarily coincide. It should be mentioned here that Blakemore and Van Sluyters (1974) report that after a period of alternating monocular occlusion, the remaining binocular cells may differ in their preferred orientations for stimulation through each eye.

These results are in agreement with classical experimental data in the domain of visual cortex development. Further, it seems likely that we can also explain other recent data obtained from more complicated paradigms such as those reported in Rauschecker and Singer (1981).

Most of the results presented in this section could be derived fairly easily, with no need of further simulations, from our knowledge of the convergence to selective states in the case of a monocularly driven neuron in a circular environment (section Va). Some intriguing properties of our theory, however, are more subtle. As an example, it is shown in Appendix C that in the MD case, the degree of monocularity of the cortical cell is correlated with its orientation selectivity as well as the diversity of inputs to the open eye. These unexpected predictions agree well with the observation by Cynader and Mitchell (1980) and Trotter et al. (in press) that after a brief period of monocular exposure, oriented cells are more monocular than non-oriented ones as well as the observation of Rauschecker and Singer (1981) that an open eye with restricted inputs leads to cells oriented to the restricted input that are less monocularly driven than usual.

VII. DISCUSSION

We propose a new mathematical form for synaptic modification and investigate its consequences on the development of selectivity in cortical

neurons. In addition we provide a definition of the notion of selectivity with respect to a random variable that might be applied in many different situations (in the domain of development of sensory systems, for example, selectivity of binocular neurons to retinal disparity, etc.) In its application to visual cortex our theory is in agreement with classical experimental results obtained over the last generation and offers a number of new predictions, some of which can be tested experimentally. This may lead to the identification of the parameters of the theory and provide indications as to the biochemical mechanisms underlying cortical plasticity.

In a broader context, we may regard our form of synaptic modification as a specific correlation modification of a hebbian type. The great majority of models on a synaptic level in domains such as pattern recognition, task learning or associative memory¹⁰ (which are less accessible to direct neurophysiological experimentation) use schemes of a hebbian type with some success. We are thus led to conjecture that some form of correlation modification is a very general organizational principle that manifests itself in visual cortex in a manner that is accessible to experiment.

Although synaptic competition is a natural consequence of Hebb's principle, its precise form must be defined. A distinction was made in Section III between spatial competition--the form commonly accepted by theoreticians as well as experimentalists--and temporal competition, the form utilized in this work. The performance of these two is very different as we see most clearly in the development of selectivity. In the temporal version

asymptotic states are of maximum selectivity with respect to the experienced environment d , independent of the geometry of d . This was rigorously proven analytically in some cases (Theorem 1; Section IV) and conjectured on the basis of numerical results in other cases (circular environments; Section V). In contrast with this, we claim that in any model using spatial competition, correct behavior strongly depends on the geometry of the environment: i.e., selective states are not reached if the patterns in the environment are not sufficiently separated from one another. Although this general statement is not proven here, a proof is sketched in Appendix B for one particular model using spatial competition between converging afferents.¹¹

We further note that selectivity, as was shown in Section VIb, does not develop in a "pure noise" environment (the distribution termed DR). Some kind of patterned input is required.¹² It follows that, even at the first level of organization of connectivity, information is being transferred from the environment to the system. This may shed some light on what has been known for a long time as the innate/learned controversy in visual cortex. Our results suggest that this dichotomy is, at best, misleading. The system's potential developmental ability--its evolutive power--may indeed be genetically determined; yet selectivity has no meaning if it does not refer to a given structured environment

that determines the final organization of the system.¹³

The present work, however, makes no assumptions concerning the initial state of cortex (e.g. the presence or absence of selectivity at eye-opening). This question, still a subject of controversy (see Pettigrew, 1978), must be settled experimentally. Further, although we here assume that all synapses are equally modifiable, it could easily be the case that there is variation in modifiability--even one that is time dependent--and that for example some of the initial state information is contained in a skeleton of synapses that is less modifiable.¹⁴

The principal results of our theory, applied to visual cortical neurons and assuming that they are all equally modifiable according to equations 4-7 are now summarized. These results are either in agreement with existing experimental data or are new and somewhat expected consequences of our theory.

A. Monocularly driven neurons

1) A monocularly driven neuron in a 'normal' (patterned) environment becomes selective. The precise pattern to which it becomes selective is determined at random if the initial selectivity is zero, or may be biased toward a particular pattern if there is a built-in preference for this pattern.

2) This same neuron in various deprived environments evolves as follows:

a) Pure noise. The neuron becomes less selective but continues to be (somewhat) responsive. It may show an orientation preference, but this is relatively unstable.

b) Exposure to a single pattern (such as vertical lines). The neuron comes to respond preferentially to the single pattern but with less selectivity (less sharply tuned) than if all orientations were present in the environment. This last is a natural consequence of temporal competition between incoming patterns and can provide a good test of our theory.¹⁵

3) Inhibitory synapses are required to produce maximum selectivity. If such inhibitory connections are arbitrarily set equal to zero, selectivity diminishes.

B. Binocularly Driven Neurons

1) A binocularly driven neuron in a 'normal' (patterned) environment becomes selective and binocular. It is selectively driven by the same pattern from both eyes.

2) This same binocularly driven neuron in various deprived environments evolves as follows:

a) Uncorrelated patterned inputs to both eyes. The neuron becomes selective, often monocularly driven; if binocular sometimes driven by different patterns from the two eyes.

b) Patterned input to one eye, noise to the other (monocular deprivation). The neuron becomes selective and generally driven only by the open eye. There is a correlation between selectivity and binocularity. The more selective the neuron becomes, the more it is driven only by the open eye. A non-selective neuron tends to remain binocularly driven. This correlation is due in part to the fact that it is the same mechanism of synaptic change that serves to increase both the selectivity and ocular dominance of the open eye. However (as shown in Appendix C) there is also a subtler connection: It is the non-preferred inputs from the open eye accompanied by noise from the closed eye that drive the neuron's response to the closed eye to zero. Thus, for example, if the visual environment were such that there were mostly preferred inputs to the open eye, even a selective cell would remain less monocular. (It should prefer the open eye but remain somewhat driven by the closed.) As another example, a kitten dark-reared to the age of about 42 days (when there remain few or no specific cells) and then given monocular exposure to non-patterned input would retain more binocularly driven cells than a similar animal given patterned input.¹⁶

c) Noise input to both eyes (Dark Rearing or Binocular Deprivation). The neuron remains non-selective (or loses its selectivity) and diminishes its responsiveness but remains binocularly driven (in contrast to the situation in monocular deprivation).

These theoretical conclusions are consistent with experimental data on increases and decreases in selectivity, data concerning changes in ocular dominance in various rearing conditions, as well as data from more complicated paradigms. Although there are indications in recent work that some of the new predictions are in agreement with experiment, they provide the opportunity for tests of more subtle aspects of the theory.

In conclusion, we note that a precise application of our theory to certain complicated experimental situations would probably require inclusion of some anatomical details, interneuronal interactions, as well as a statement of what information is innate and which synapses are modifiable.¹⁷

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Appendix A: Biochemical Mechanism for Temporal Competition

It is probably premature to propose a detailed physiological mechanism for a mathematical synaptic modification algorithm: too many possibilities exist with no present experimental test to decide between them. However, we propose the following as a possible example.

The dependence of our modification threshold upon the mean postsynaptic activity--which regulates the individual neuron modification in an overall manner--might be the result of a physiological mechanism within the framework proposed by Changeux et al. (1973). Their basic hypothesis is that receptor protein on the postsynaptic membrane exists in two states, one labile, the other stable; selective stabilization of the receptor takes place during development, in an activity-dependent fashion. The quantity of labile receptor available for stabilization is determined by the neuron's average activity, i.e., labile receptor is not synthesized anymore when the neuron's activity is high for a relatively long period of time ($\bar{c} \gg c_0$). (Cf. Changeux and Danchin (1976): "The activity of the postsynaptic cell is expected to regulate the synthesis of receptor".)

Our hypothesis that during the period when competition really takes place (i.e., when \bar{c} is of the order of c_0 in eq. 7) the sign of the modification is determined by the instantaneous activity, c , relative to its mean, \bar{c} , requires that a single message, the instantaneous activity, be fed back from the site of integration of the incoming message to the individual synaptic sites, on a rapid time-scale, i.e., much faster than the one

involved in the overall regulation mechanism. This might be contrasted with the assumption implicit in most spatial competition models, namely, that a chemical substance is redistributed between all subsynaptic sites (cf. the principle of conservation of total synaptic strength (von der Malsburg, 1973)).

Appendix B: Von der Malsburg's model of development of orientation selectivity

A model of development of orientation selectivity using an evolution scheme of the spatial type may be found in von der Malsburg (1973). We present here a brief analysis of this model in view of the definition given in Section III. We first show that the type of competition implied by this model is indeed formally, the spatial one. Next we investigate the behavior of the system in the simple situation of Theorem 1 in Section IV, i.e., for a two-pattern environment, the dimension of the system being $N = 2$: We will show why the assumption that is made of nonlinearity of the integrative power is a necessary one. Finally, we prove that the class of two-pattern environments \underline{d} in which the system behaves nicely, i.e., the state is asymptotically selective with respect to \underline{d} , is defined by a condition of the type $0 < \cos(d^1, d^2) < a$, where d^1 and d^2 are two patterns in \underline{d} , and a is a constant strictly less than 1, which actually depends on the nonlinearity of the integrative power, i.e., on its threshold θ .

For the purpose of our analysis, we consider a single "cortical" neuron, whose integrative and evolutive power are--in our notation--the following:

$$c_j(t) = (m_j(t) \cdot d_j(t))^*, \quad (B1)$$

with

$$u^* = \begin{cases} u - \theta & \text{if } u > \theta \\ 0 & \text{if } u < \theta \end{cases} \quad (B2)$$

$$m_j(t+1) = \gamma_j(t+1)(m_j(t) + h_j c_j(t) d_j(t)) \quad j=1, \dots, N \quad (B3)$$

With h a small positive constant and $\gamma(t+1)$ such that:

$$\sum_{j=1}^N \bar{w}_j(t+1) = \sum_{j=1}^N \bar{w}_j(t) = s \quad (B4)$$

The integrative power is thus nonlinear, with threshold θ . The normalizing factor $\gamma(t+1)$ in the evolution equation (12), keeps the sum of synaptic weights constant, equal to s . All variables are positive.

Our analysis will be carried out on this reduced version of von der Malsburg's model: we simply ignore the fixed intracortical connections assumed there, for these are clearly not sufficient to tune the system to a selective state if individual neurons don't already display this property as is clearly stated by the author himself, the ability to develop selectivity is an intrinsic property of individual neurons, the intracortical connections being there to organize orientation preference in a coherent way in cortex. (This also the viewpoint in the present work: see Appendix D). Notice that this is by no means a contradiction to the fact that in the final state, intracortical connections, particularly the inhibitory ones, significantly contribute to the selectivity of each neuron.

A straightforward calculation shows that eqs. B3 and B4 are equivalent to the following.

$$\begin{cases} \bar{w}_j(t+1) - \bar{w}_j(t) = K(t) (\bar{d}_j(t)/\bar{d}(t) - \bar{w}_j(t)/s) & j = 1, \dots, N \\ K(t) = s h \bar{c}(t) \bar{d}(t) / (s + h \bar{c}(t) \bar{d}(t)), \end{cases} \quad (B5)$$

where $d(t) = \sum_{j=1}^N d_j(t)$. (In the simulations, $d(t)$ is actually a constant.)

Thus, according to eq. B5, the sign of the change of m_j at time t does not depend on the postsynaptic activity $c(t)$ but on the j -th fiber activity, $d_j(t)$. This is clearly spatial competition, as was intuitively clear from the conservation law (eq. B4).

We investigate now the behavior of system B5 in a two-pattern environment: $P[d=d^1] = P[d=d^2] = .5$. For this purpose we slightly modify the original setup: there the dimension is relatively high ($N=19$) but the firing frequencies in the afferent fibres are discrete-valued, i.e., $d_j = 0$ or 1, $j=1, \dots, N$. Here, we take $N=2$ with $d_{1,2}$ allowed to take any value between 0 and 1. We thus still get a broad range of environments ($\cos(d^1, d^2)$ may assume any value between 0 and 1), but the analysis is made considerably easier. To further simplify, we characterize d by a single parameter $0 < \delta < 1$ by writing $d^1 = (1, \delta)$, $d^2 = (\delta, 1)$. Thus $\cos(d^1, d^2) = 2\delta/(1+\delta^2)$. We also set $s = 1$.

Under these circumstances, averaging the evolution equation B5 with respect to d leads to the following:

$$E[m_j(t+1) - m_j(t)] = h(2m_j(t) - 1) (\theta(1+\delta) - 2\delta), \quad j=1,2. \quad (B6)$$

To obtain eq. B6, it has been assumed that both inputs yield above-threshold responses, i.e., $m \cdot d^1$ and $m \cdot d^2 > 0$. Higher order terms in h have been ignored.

We see that the behavior of the system is determined by the sign of the quantity $\theta(1+\delta)-2\delta$. Notice that, since $s=1$, θ cannot be arbitrarily high: in order that states m exist such that $m \cdot d^1$ and $m \cdot d^2 > 0$, one has to assume that $\theta < (1+\delta)/2$.

It follows from eq. B6 that for δ such that $\theta(1+\delta)-2\delta < 0$, there is one attractor of selectivity 0, namely (.5; .5). When δ gets smaller and $\theta(1+\delta)-2\delta$ becomes positive, the solution bifurcates into two attractors of maximum selectivity. We thus conclude that:

1. If the neuron's integrative power is linear, i.e., $\theta=0$, the asymptotic state is nonselective. (When $\theta=0$ and d^1 and d^2 are orthogonal, (i.e., $\delta=0$) the first-order term in h vanishes, yet the second-order term also leads to the nonselective fixed point.)

2. Given a fixed $0 < \theta < 1$, the environments d that are acceptable to the system are those which satisfy $\delta < \theta/(2-\theta)$, which is equivalent to a condition of the type $\cos(d^1, d^2) < a$, with a strictly less than 1. (Notice that in the actual simulations, d consists of 9 stimuli that are indeed well separated from one another, since $\min_i \cos(d^1, d^i) = 1/7$.)

Appendix C: Correlation Between Ocular Dominance and Selectivity in the Monocular Deprived Environment.

Consider the MD environment in Section VIb: it is defined by (d_r, n) where d_r is circular and n is a "pure noise" vector. We will prove that the state $(m_r^*, 0)$ is stable in this environment provided that m_r^* is a stable selective state in the environment d_r .

Let (x_r, x_l) be a small perturbation from equilibrium. The motion at point $(m_r^* + x_r, x_l)$ is given by:

$$\dot{x}_r = \phi(m_r^* \cdot d_r + x_r \cdot d_r + x_l \cdot n, m_r^* \cdot \bar{d}_r + x_r \cdot \bar{d}_r) d_r \quad (C1r)$$

$$\dot{x}_l = \phi(m_r^* \cdot d_r + x_r \cdot d_r + x_l \cdot n, m_r^* \cdot \bar{d}_r + x_r \cdot \bar{d}_r) n \quad (C1l)$$

where we assume that the noise has zero mean.

We analyze separately--somewhat informally--the behavior of the two equations. The stability of eq. C1r is immediate from the stability of the selective state m_r^* in the circular environment d_r . To analyze C1l, we divide the range of the right eye input d_r into three classes:

- (i) d_r is such that $m_r^* \cdot d_r$ is either far above threshold, θ_M , and therefore $\phi(m_r^* \cdot d_r, m_r^* \cdot \bar{d}_r) > 0$, or far below threshold, θ_M , (but still positive) and therefore $\phi(m_r^* \cdot d_r, m_r^* \cdot \bar{d}_r) < 0$;
- (ii) d_r is such that $m_r^* \cdot d_r$ is near threshold, θ_M , and therefore $\phi(m_r^* \cdot d_r, m_r^* \cdot \bar{d}_r) \approx 0$

$$(iii) \quad d_r \text{ is such that } m_r^* \cdot d_r \approx 0 \text{ and again} \\ \phi(m_r^* \cdot d_r, m_r^* \cdot \bar{d}_r) \approx 0.$$

For the first class of inputs, the sign of ϕ is determined by d_r alone, hence Cl1 is the equation of a random walk. To investigate the behavior of Cl1 in the two other cases, we neglect the term x_r and linearize ϕ around the relevant one of its two zeros. It is easy to see that case (ii) yields

$$\dot{x}_l \approx \epsilon_1 (x_l \cdot n) n, \quad (C2)$$

whereas in case (iii) one obtains

$$\dot{x}_l \approx -\epsilon_2 (x_l \cdot n) n, \quad (C3)$$

where ϵ_1 and ϵ_2 are positive constants, measuring respectively the absolute value of the slope of ϕ at the modification threshold and at 0.

Since n is a noise-like term, its distribution is presumably symmetric with respect to x_l and averaging eqs. (C2) and (C3) yields respectively

$$\dot{x}_l \approx \frac{1}{N} \epsilon_1 n^2 x_l \quad (C4)$$

$$\dot{x}_l \approx -\frac{1}{N} \epsilon_2 n^2 x_l \quad (C5)$$

where n^2 is the average squared magnitude of the noise input to the synapses from the closed eye and N is the dimensionality of the system.

We thus see that input vectors from the first class move x_l randomly, inputs from the second class drive it away from 0, whereas inputs from the third

drive it toward 0. The random contribution occurs only before the synaptic strengths from the open eye have settled to one of their fixed points. Once these strengths have reached a fixed point, only (ii) and (iii) occur. In the case where the range of d_r is a set of K linearly independent vectors and m_r^* is of maximum selectivity, $(K-1)/K$, case (i) does not occur at all. Case (ii) occurs only for one input, say d_r^1 , with $m_r^* \cdot d_r^1$ exactly equal to threshold, ϕ_M , and (iii) occurs for the other $K-1$ vectors which are all orthogonal to m_r^* . The more selective m_r^* with respect to d_r , the higher the proportion of inputs belonging to class (iii), the class that yields eq. C5, i.e., that brings x_{ℓ} back to 0.

The stability of the global system still depends on the ratio of the quantities ϵ_1 and ϵ_2 as well as on the statistics of the noise term n_{\sim} (e.g. its mean square norm). We may however formulate two general conclusions. First, under reasonable assumptions (ϵ_1 of the order of ϵ_2 and the mean square norm of n_{\sim} of the same order as that of d_r) $x_{\ell} = 0$ is stable on the average for a selective m_r^* . Second, the residual fluctuation of x_{ℓ} around 0, essentially due to inputs d_r in classes (i) and (ii), is smaller for highly selective m_r^* 's than it is for mildly selective ones.

Thus, one should expect that in a monocularly deprived environment non-selective neurons tend to remain binocularly driven. In addition since it is the non-preferred inputs from the open eye accompanied by noise from the closed eye (case three) that drive the response to the closed eye to zero, if inputs to the open eye were restricted to preferred inputs (case two) even a selective cell would remain less monocular.

Appendix D: Many Neuron Systems

It is very likely that interactions between cortical neurons play an important role in overall cortical function as well, perhaps, as in selectivity of individual cortical cells (Creutzfeldt et al., 1974 and Sillito, 1975). Although in this paper we have treated the development of selectivity of cortical neurons with inputs only from geniculate neurons, the input space can be generalized to include inputs from other cortical neurons as well. Thus the ideas and methods employed here are equally applicable to the many-neuron system. Most important, the result that stable equilibria in a stationary environment are selective with respect to their environment can be taken over to the many-neuron system.

Consider such a system in a stationary external environment. The state of each cortical neuron now has two parts: one relative to the geniculocortical synapses, the other to the cortico-cortical ones. The environment of the neuron is no longer stationary, for the states of all other cortical neurons in the system evolve. Yet, when the system reaches global equilibrium, which will occur under reasonable assumptions, each individual environment becomes stationary. The single unit study then allows us to state that, at least in principle, (we don't know a priori that each environment is circular) the state of each neuron is selective with respect to its own individual environment.

In practice, formulation of the many-neuron problem poses two questions. First, the integrative power of the system should be specified. Since

the system includes cortico-cortical loops, it is not obvious what the response to a given afferent message should be. The two major alternatives are: a. Stationary cortical activity is rapidly reached, (i.e., before the afferent message changes); b. Relevant cortical activity is transitory. The second question concerns the evolution of cortico-cortical synaptic strengths: should these synapses be regarded as modifiable at all and if yes, how? Van der Malsburg (1973), assumes (a) above and proposes fixed connectivity patterns, short-range excitatory, longer-range inhibitory.

We have performed a simulation of a many-neuron system using the much simpler (and probably more natural) assumption (b) above: 1. Only monosynaptically and disynaptically mediated components of the afferent message are taken into account for the computation of each cortical neuron's activity, before modification is performed and a new stimulus is presented. 2. Intracortical connections are fixed, and spatially organized as in von der Malsburg (1973). 3. The state of each neuron evolves according to eqs. 6 and 7 of the present work. The results are the following:

1. The system's state converges.
2. At equilibrium, each neuron stands in a selective state with respect to the environment.
3. Preferred orientation--when the environment is a circular one--is a piecewise continuous function of cortical distance. Point 3 is illustrated in Fig. 6.

FOOTNOTES

3. The precise form of the averaging integral, i.e. of the convolution kernel, is not essential. Exponential kernels $K(t) = \exp(-t/\tau)$ are often used in this context (see e. g. Nass and Cooper, 1975; Uttley, 1976).
4. The mathematical concept that is needed in order to represent the environment, d_{ω} , during the development period is that of a stationary stochastic process, $d_{\omega}(t)$, that is (roughly), a time-dependent random variable whose distribution is invariant in time. For example, d_{ω} could represent an elongated bar in the receptive field of the neuron, rotating in some random manner around its center. At each instant, the probability of finding the bar in any given orientation is the same as at any other: the distribution of $d_{\omega}(t)$ is time-invariant, uniform over the interval $(0, 180^{\circ})$.
5. Nonspecific conditions for synaptic decrease such as uniform exponential decay is clearly insufficient too: in Nass and Cooper (1975) for instance, no selectivity is achieved without lateral intracortical inhibition. Other models (von der Malsburg, 1973; Perez et al., 1975) use a normalization rule in conjunction with a hebbian scheme for synaptic increase, which actually results in decrease as well as increase. This normalization rule is discussed in Appendix B.
6. Replacing the time average by an average over the distribution of d_{ω} is allowed provided that 1) the process $d_{\omega}(t)$ is stationary, 2) the

interval, T , of time integration is short with respect to the process of synaptic evolution (i.e., $p(t)$ changes very little during an interval of length T), 3) T is long compared to the mixing rate of the process d (i.e. during a period of length T , the relative time spent by the process $d(t)$ at any point d in the input space is nearly proportional to the weight of the distribution of d at d). Now, synaptic evolution is probably a slow process, requiring minutes or hours (if not days) to be significant, whereas elementary sensory patterns (e.g. oriented stimuli in the receptive field of a given cortical neuron) are normally all experienced in an interval of the order of, say, 1 min. or less. We are thus able to choose T so that a good estimate of $\bar{c}(t)$ be available to the neuron.

7. The sign of $\phi(c, \bar{c})$ for $c < 0$ is not crucial since c is essentially a positive quantity: cortical cells in general have low spontaneous activity and at any rate are rarely inhibited much below their spontaneous activity level. For the sake of mathematical completeness, one may however wish to define $\phi(c, \bar{c})$ for negative c ; $\phi(c, \bar{c}) > 0$ is then the most convenient for it allows to state theorems 1-3 below under the most general initial conditions.
8. The circular environment which serves to assess the orientation tuning curves is now in a sense arbitrary, since it is not at all used in the development period. The same remark applies of course to the BD case.
9. In fig. 1B of Fregnac and Bienenstock (1981), which shows averaged orientation tuning curves of a cell recorded in an 86 day old DR cat, the selectivity is .58 at the beginning of the recording session, and .28 at the end.

10. Notice, for instance, the analogy between states of maximum selectivity as defined here and the optimal associative mappings of Kohonen (1977).
11. More complicated temporal or mixed spatio-temporal schemes are possible and some such have been proposed. For example, Sejnowski (1977a) has suggested a form of modification in which the change of the j -th synaptic strength involves the covariance between the j -th fiber and post-synaptic activities (Sejnowski, 1977a). In addition, interaction between neurons (such as lateral inhibition) can increase selectivity (see for example, Nass and Cooper (1975) and Appendix D.)
12. Pure noise and circular environments may be regarded as two extreme cases: the first totally lacks structure whereas the second is highly organized. Intermediate cases, i.e., environments consisting of the sum of a noise process and of a circular process have also been investigated (see, for example, Bienenstock (1980)). There it is shown that the asymptotic selectivity directly depends on a parameter that measures the degree of structure of the environment.
13. We note, further, that the mechanism of synaptic modification we have proposed leads both to what are sometimes called 'selective' and 'instructive' effects (depending on the structure of the environment and the genetic initial state). Thus, as is already suggested by Rauschecker and Singer (1981), this dichotomy is obscured, or does not appear at all, at the synaptic level.

14. This skeleton might consist primarily of the contralateral pathway and favor the development of orientation preference for horizontally and vertically oriented stimuli. See, for example, Fregnac (1979).
15. In addition the principle of temporal competition suggests an experimental paradigm that could be used to increase the selectivity of a cortical neuron while recording from the same neuron. The paradigm consists of controlling the postsynaptic activity of the neuron while presenting sequentially in its receptive field two stimuli, A and B. Stimulus A (respectively B) should be associated with a high (respectively low) instantaneous firing rate in such a way as to keep the cell's mean firing rate at its original value. We predict that the cell will eventually prefer Stimulus A (i.e. exhibit selectivity with respect to the discrete environment consisting of A and B). An experiment based on this paradigm is currently being undertaken by one of the authors (EB) in collaboration with Yves Frégnac at the College de France.
16. In this situation one might have to distinguish between short and long monocular exposures. In very long monocular exposures the decay term of eq. 4 ($-cm(t)$) could eventually produce decay of junctions from the closed eye independent of the effect discussed above.
17. This last might be treated as for example in Cooper, Lieberman and Oja (1979).

Figure Captions

Figure 1: Computing the selectivity with respect to an environment uniformly distributed between ω_{\min} and ω_{\max} .

The abscissa displays a parameter of the stimulus, e.g. orientation ($\omega_{\max} - \omega_{\min} = 180^\circ$), the ordinate the neuron's response 0 is the level of average spontaneous activity; M is the maximum response. The selectivity of the neuron is then given by

$$\text{Sel}_d(N) = 1 - \frac{1}{M(\omega_{\max} - \omega_{\min})} \int_{\omega_{\min}}^{\omega_{\max}} f(\omega) d\omega = \frac{\text{light area}}{\text{total box area}}$$

This is a simple measure of the breadth of the peak: curves of same selectivity have approximately the same half-width at half-height. (Think for instance of triangularly shaped tuning curves.)

Typical values for orientation selectivity of adult cortical cells vary between 0.7 and 0.85. ("specific" cells). Selectivity of broadly tuned but still unimodal cells, e. g. those termed "immature" by Buisseret and Imbert (1976) and Fregnac and Imbert (1978), lies between .5 and .7. Obviously, 0 is the selectivity of an absolutely flat curve, whereas 1 is the selectivity of a Dirac δ -function.

Figure 2: A function satisfying condition (7).

The 3 diagrams show the behavior of $\phi(c, \bar{c})$ as a function of c for three different constant values of \bar{c} . In each diagram, the solid part of the curve repre-

sents $\phi(c, \bar{c})$ in the vicinity of \bar{c} , which of course is the relevant part of this function. In the upper diagram ($\bar{c} \gg c_0$), although $\phi(c, \bar{c})$ is not negative for all c as was formally required (see text), the probability that $\phi(c, \bar{c}) > 0$ is small and gets even smaller as \bar{c} increases. The important point in the definition of ϕ is the nonlinearity of $\theta_M(\bar{c})$ which makes it increase or decrease faster than \bar{c} , while $\theta_M(\bar{c})$ is of the same order as \bar{c} , if \bar{c} itself is of the same order as c_0 .

Figure 3: The phase portrait of Eq. 6 in an environment consisting of 2 inputs d^1 and d^2 (Theorems 1 and 2).

The diagram shows the trajectories of the state of the system, starting from different initial points. This is a computer simulation performed with one given function ϕ satisfying condition 7. Using a different function may slightly change the shape of the trajectories, without any essential change in the behavior. The unstable fixed points are $m^{1,2}$ and m^0 , the stable ones m^1 and m^2 . The system is a stochastic one, which means that the trajectories depend in fact on the precise sequence of inputs. As long as the state is in the unshaded region, it is not yet known whether it will eventually be attracted to m^1 or m^2 . This becomes determined as the state enters one of the trap (shaded) regions, F^1 or F^2 . Trajectories shown here are deterministic ones, obtained by alternating d regularly between d^1 and d^2 . They are in fact the averaged trajectories of the state and are much more regular and smooth than the actual stochastic ones.

Figure 4: The evolution of a synaptic system in a circular environment.

Here, $K = 40$, and the vectors are linearly dependent. The value of the maximum selectivity with respect to d is therefore not precisely

calculable. The asymptotic selectivity is approximately .9, perhaps the maximum selectivity. (a) demonstrates the progressive buildup of the selectivity in a circular environment while (b) shows the resulting tuning curve at $t = 1000$.

Figure 5: Results of computer simulations corresponding to various rearing conditions.

In these simulations the upper and lower figures show cell responses to stimuli from the two eyes.

- a) Normal (NR). The cell's response is binocular and selective.
- b) Dark rearing (DR). No stable selectivity in the cell's response. The response curve fluctuates randomly. The cell is on the average binocularly driven.
- c) Binocular deprivation (BD). The cell reaches a final state corresponding to the arbitrary vector corresponding to a diffuse input to the retina. The cells are sometimes monocularly driven. This is somewhat analogous to (e) below.
- d) Monocular deprivation (MD). The cell's response is monocular and selective.
- e) Uncorrelated Rearing (UR). Both binocular and monocular selective final states are observed.

Figure 6: A regular distribution of preferred orientation in a one-dimensional cortex.

The system is an array of 50 "cortical" cells arranged in a cyclic way (cell no. 1 and cell no. 50 are neighbors) and interconnected according to a fixed short-range-excitation-long-range-inhibition pattern. (Coefficients of interactions are, as a function of increasing inter-cell distance: .4, .4, -.2, -.4, -.4, 0, ...). The environment d of the system is the usual circular one. Integrative and evolutive powers are described in the text. When the system reaches equilibrium, one has $.73 \leq \text{Sel}_d(m_i) \leq .77$ for all i between 1 and 50. The diagram shows preferred orientation as a function of cortical coordinate.

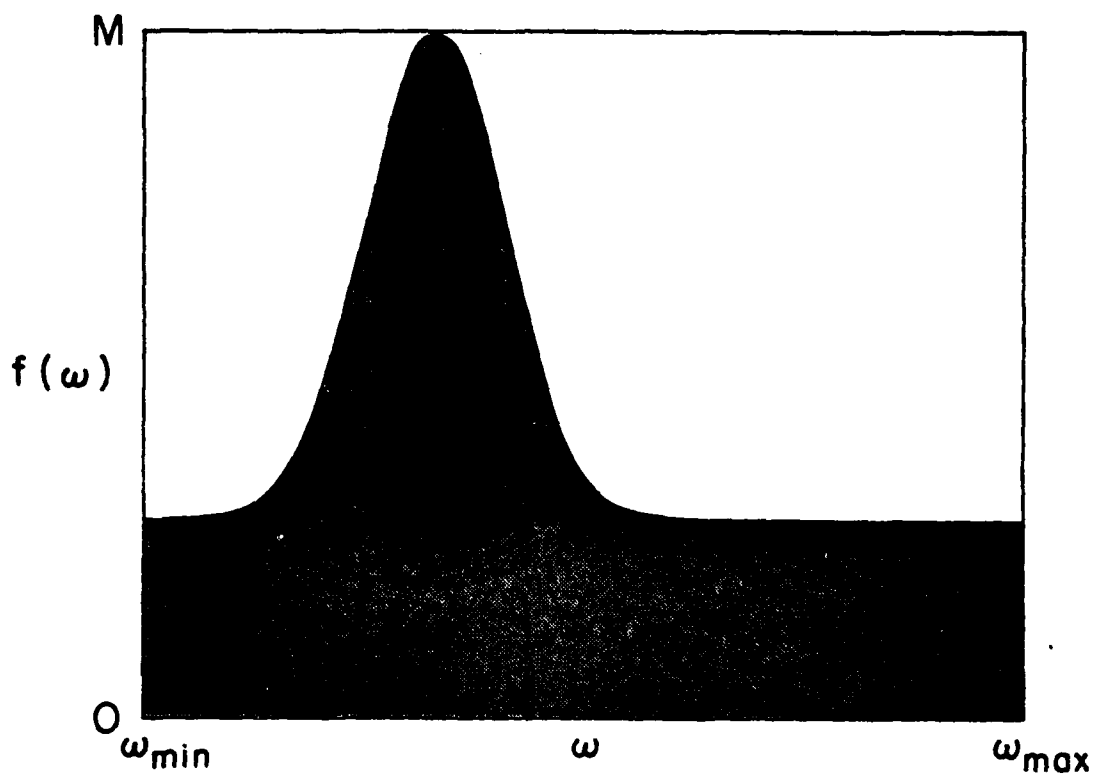


Figure 1.

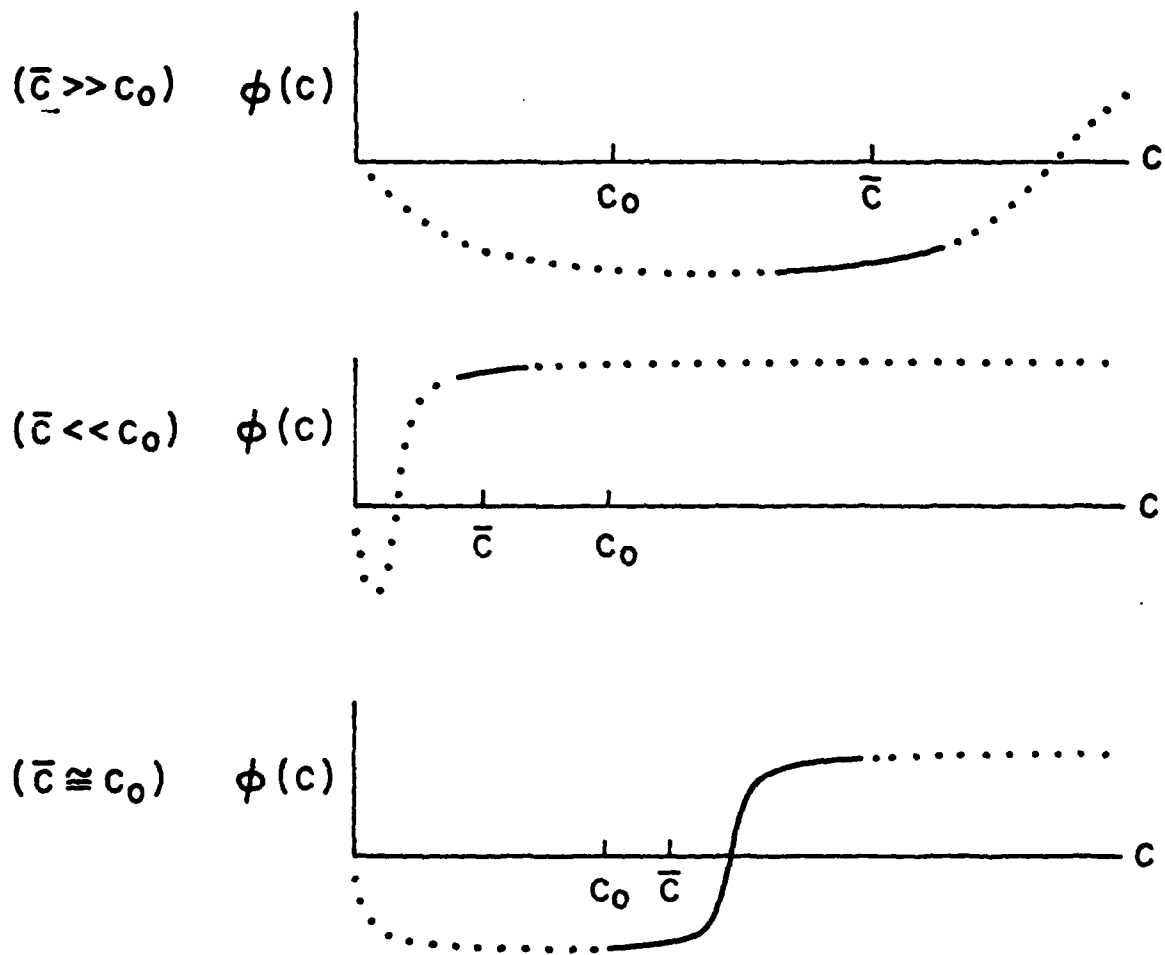


Figure 2.

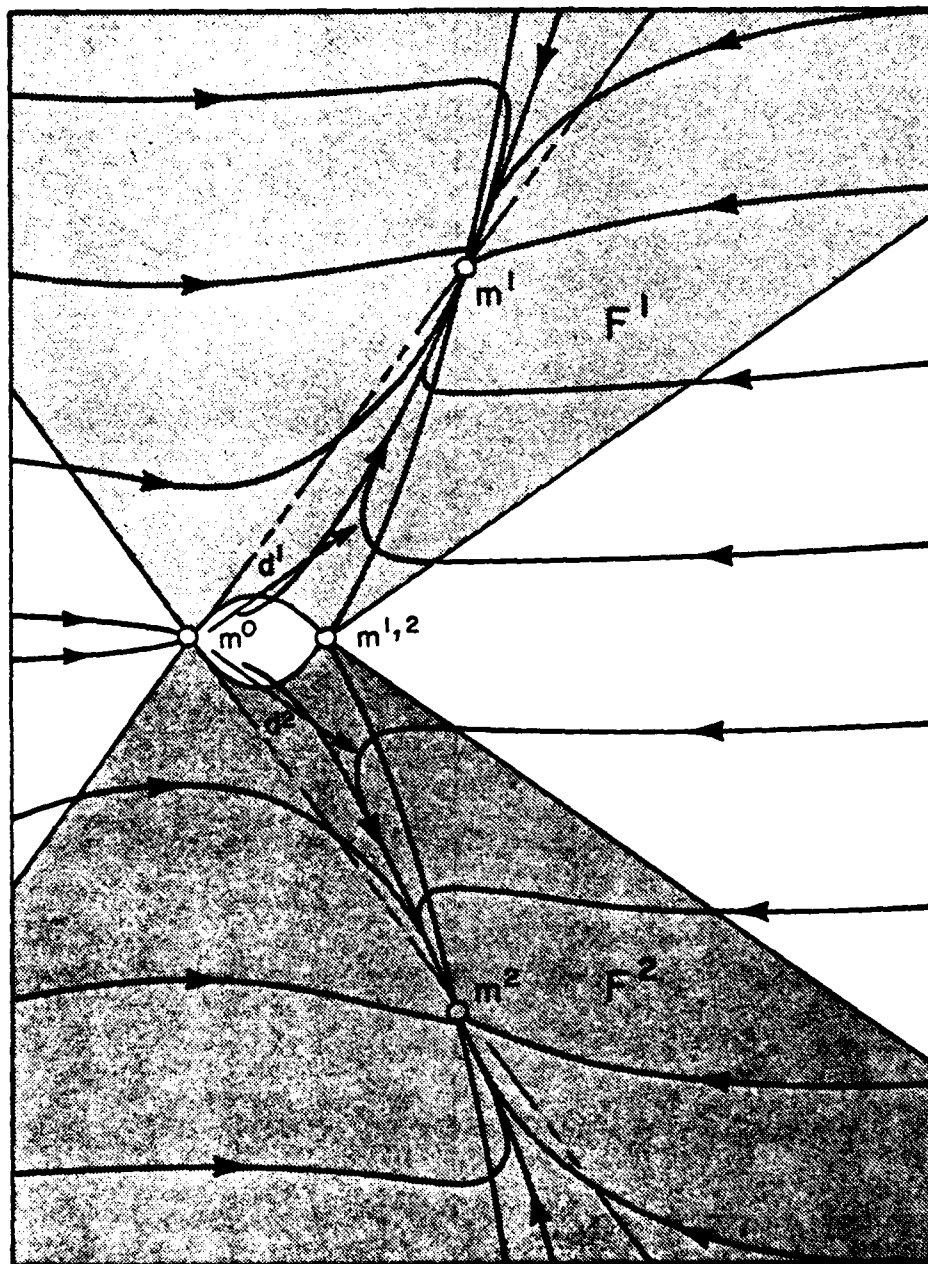


Figure 3.

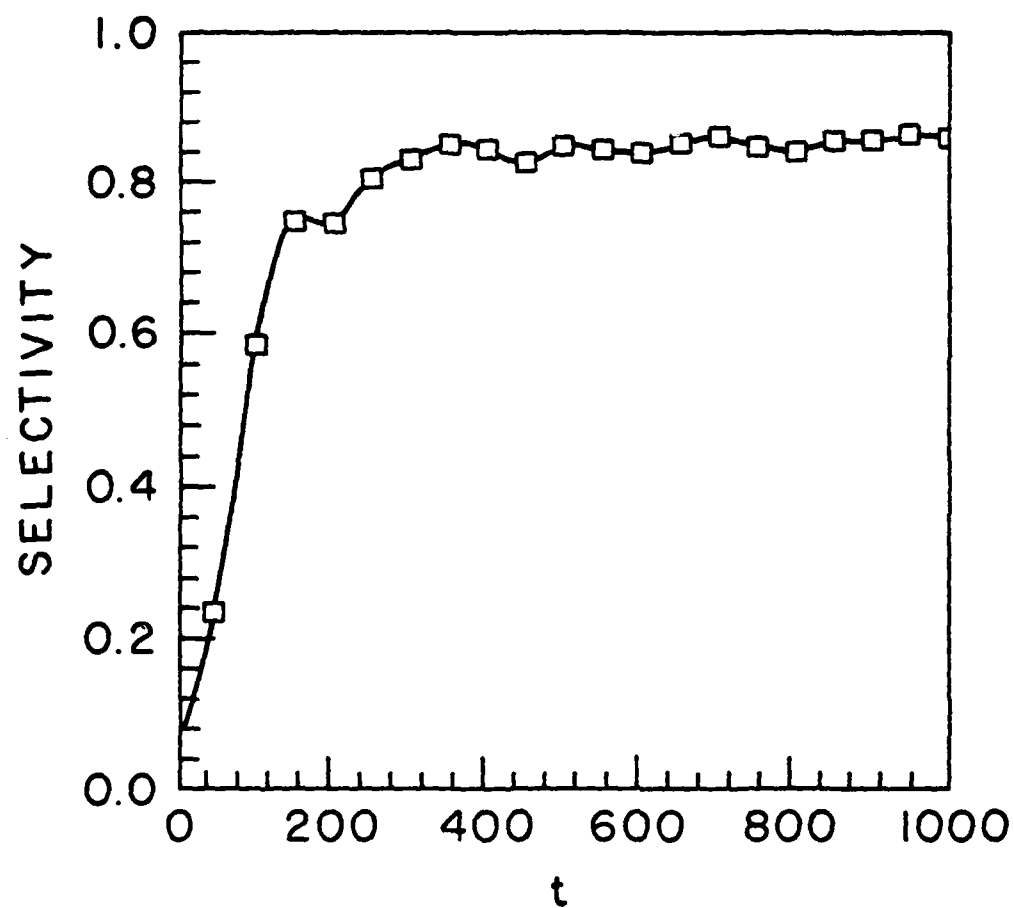


Figure 4a.

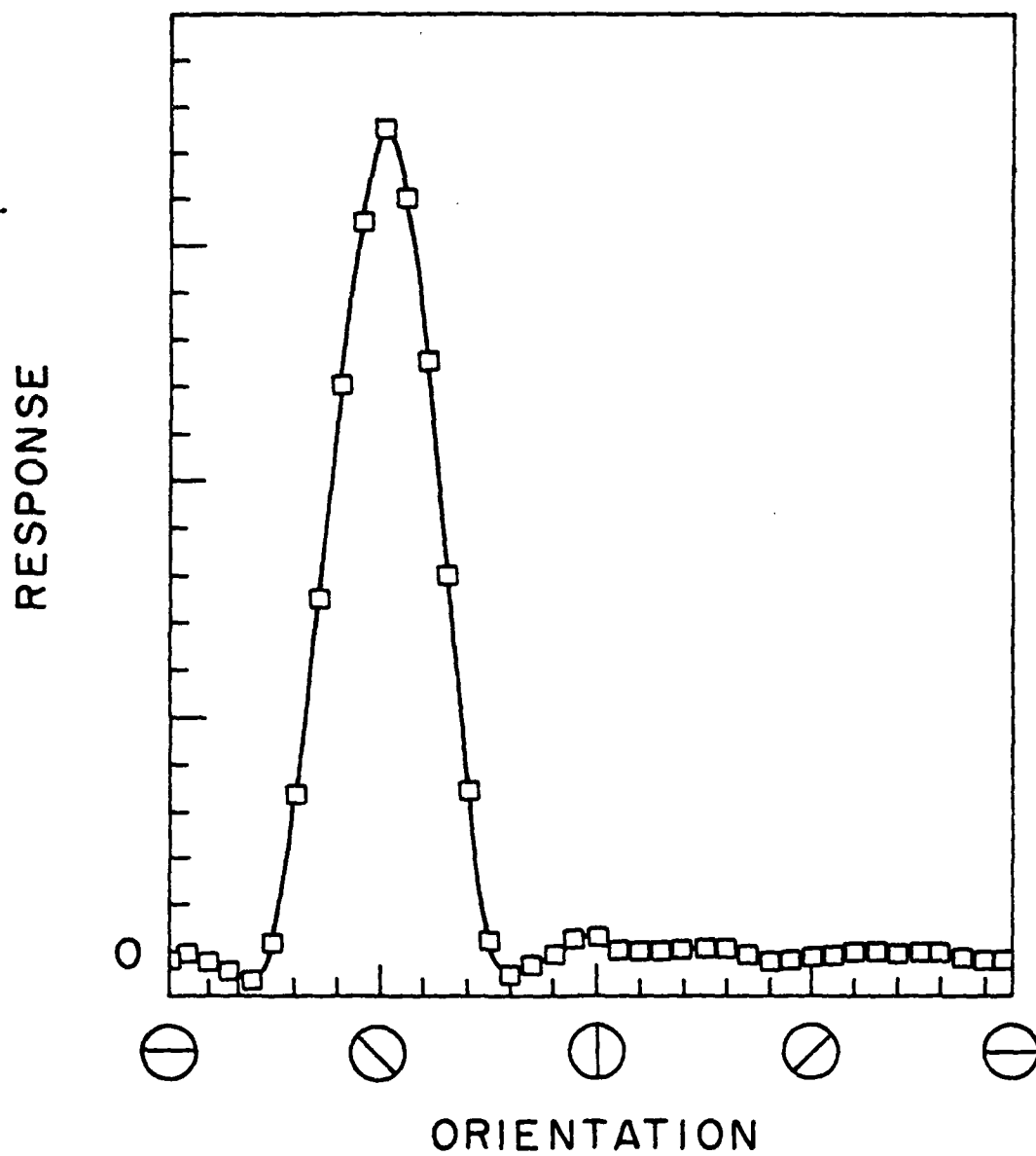


Figure 4b.

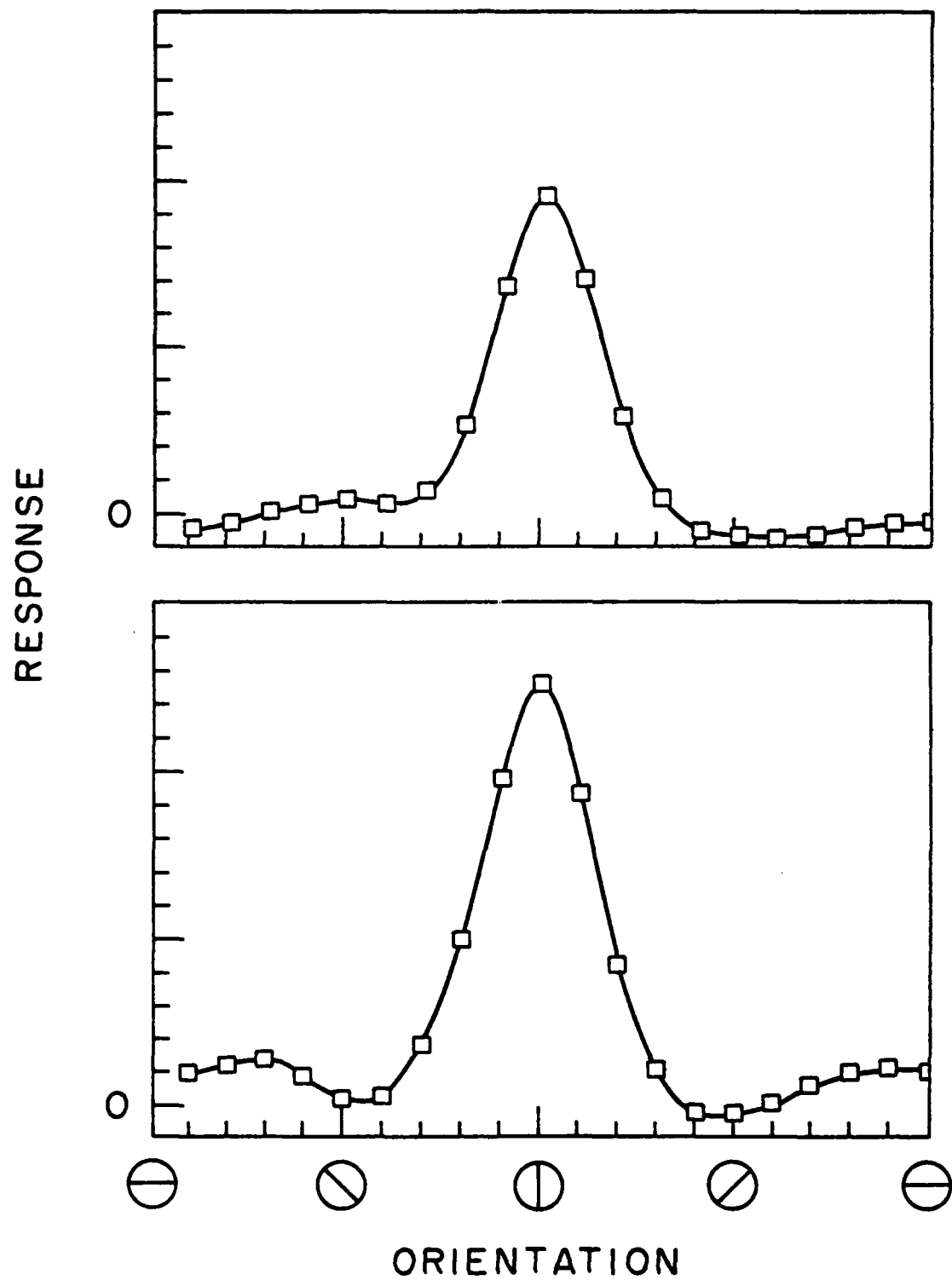


Figure 5a.

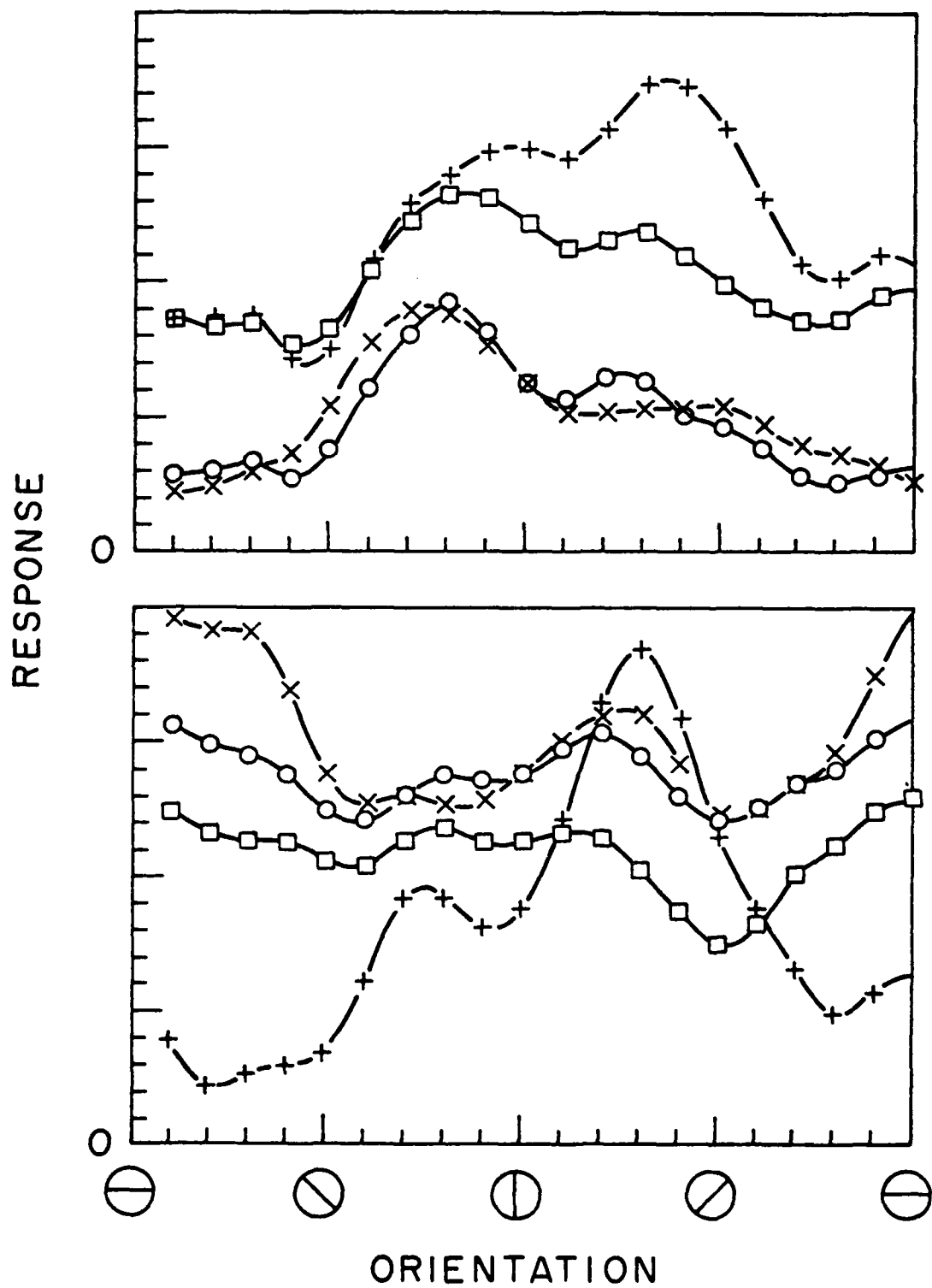


Figure 5b.

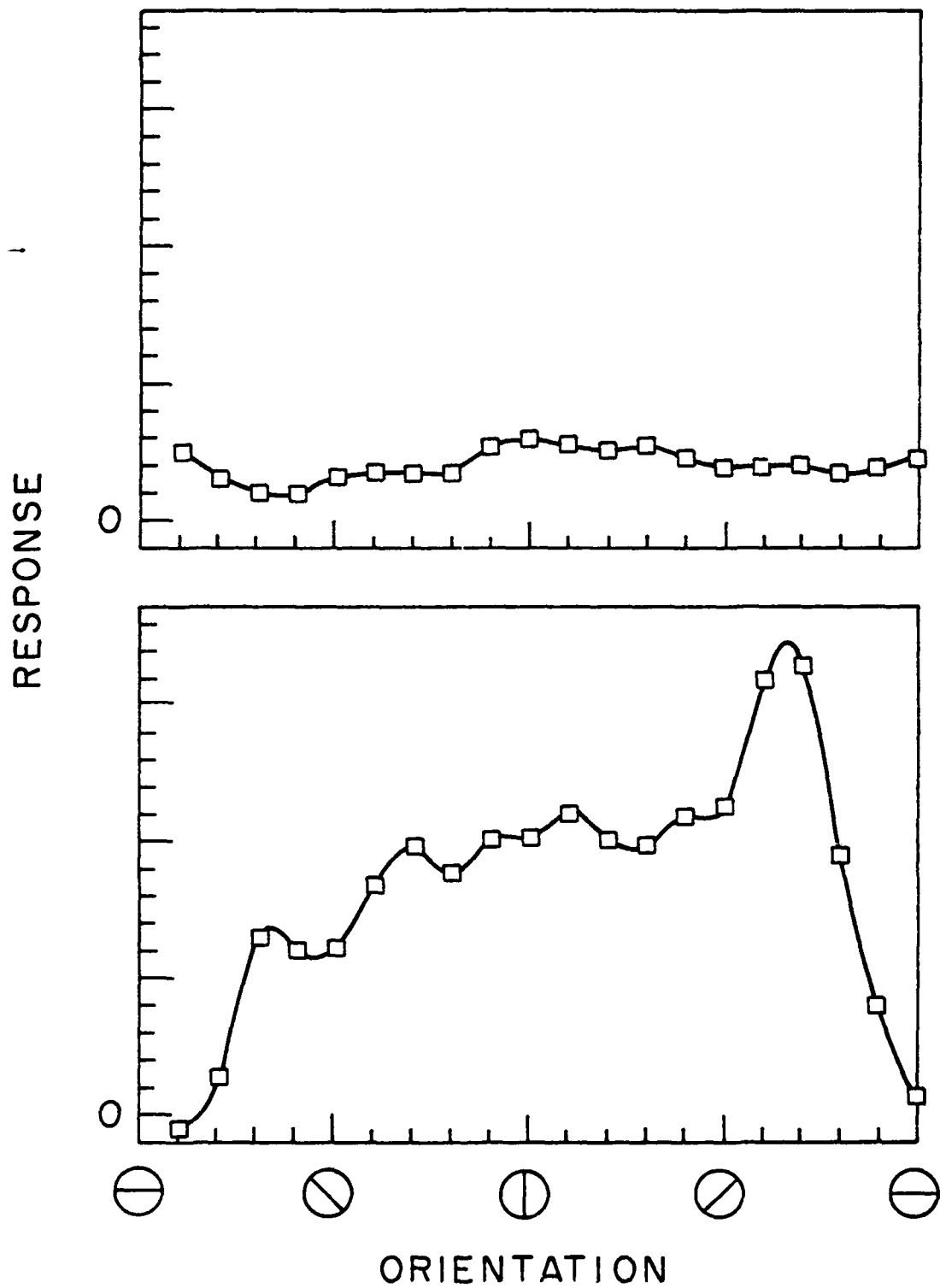


Figure 5c

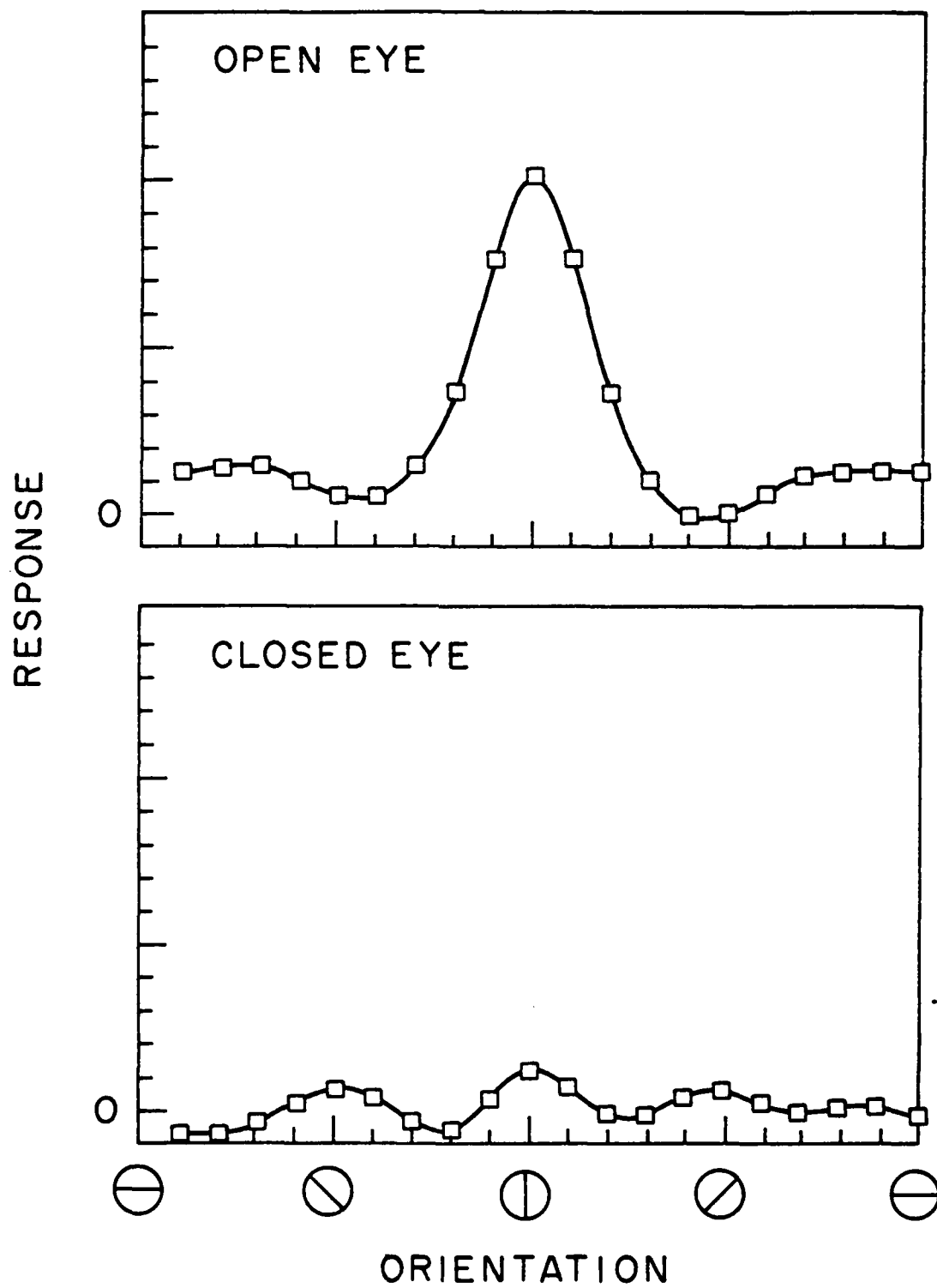


Figure 5d.

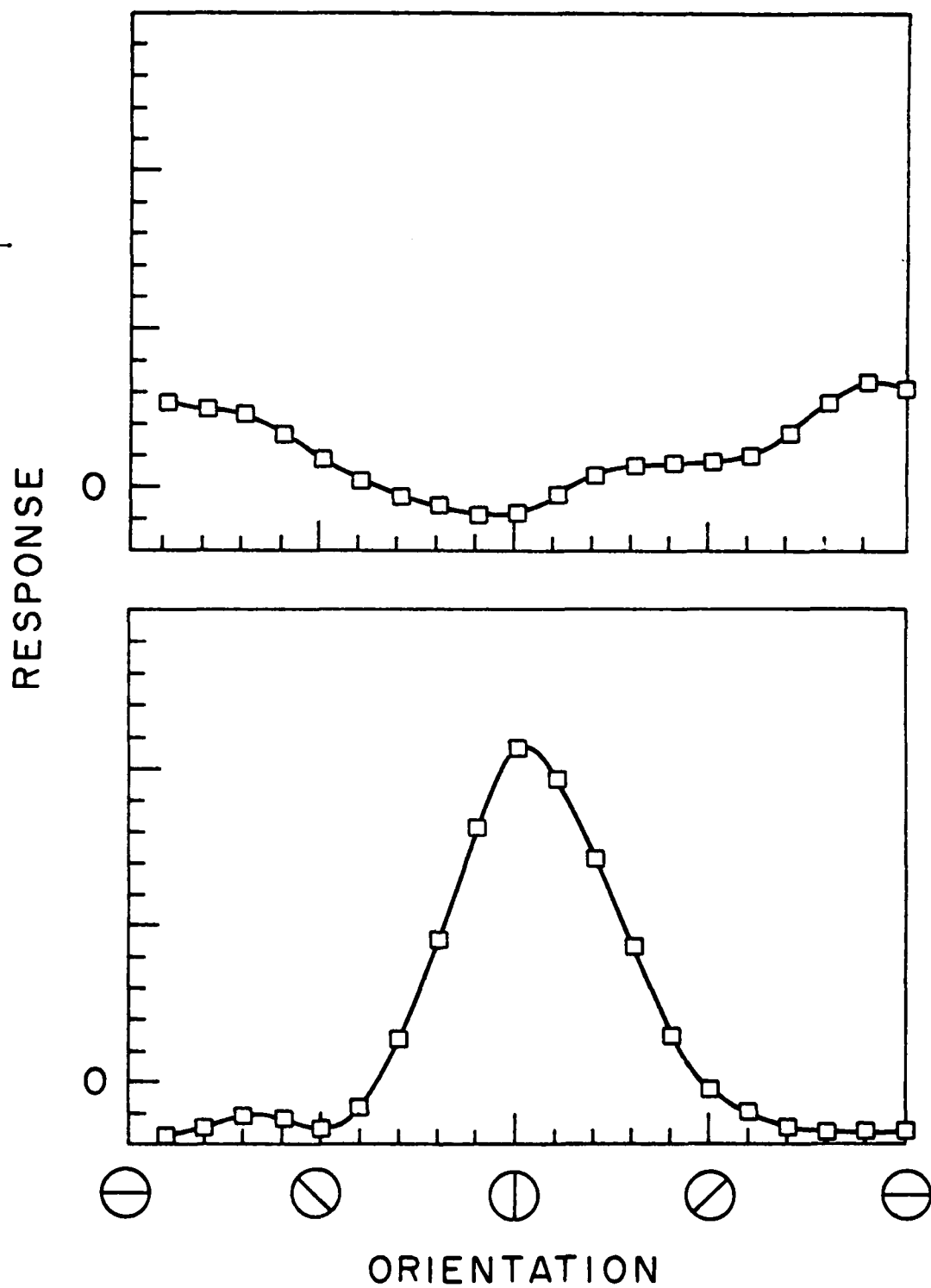


Figure 5e.

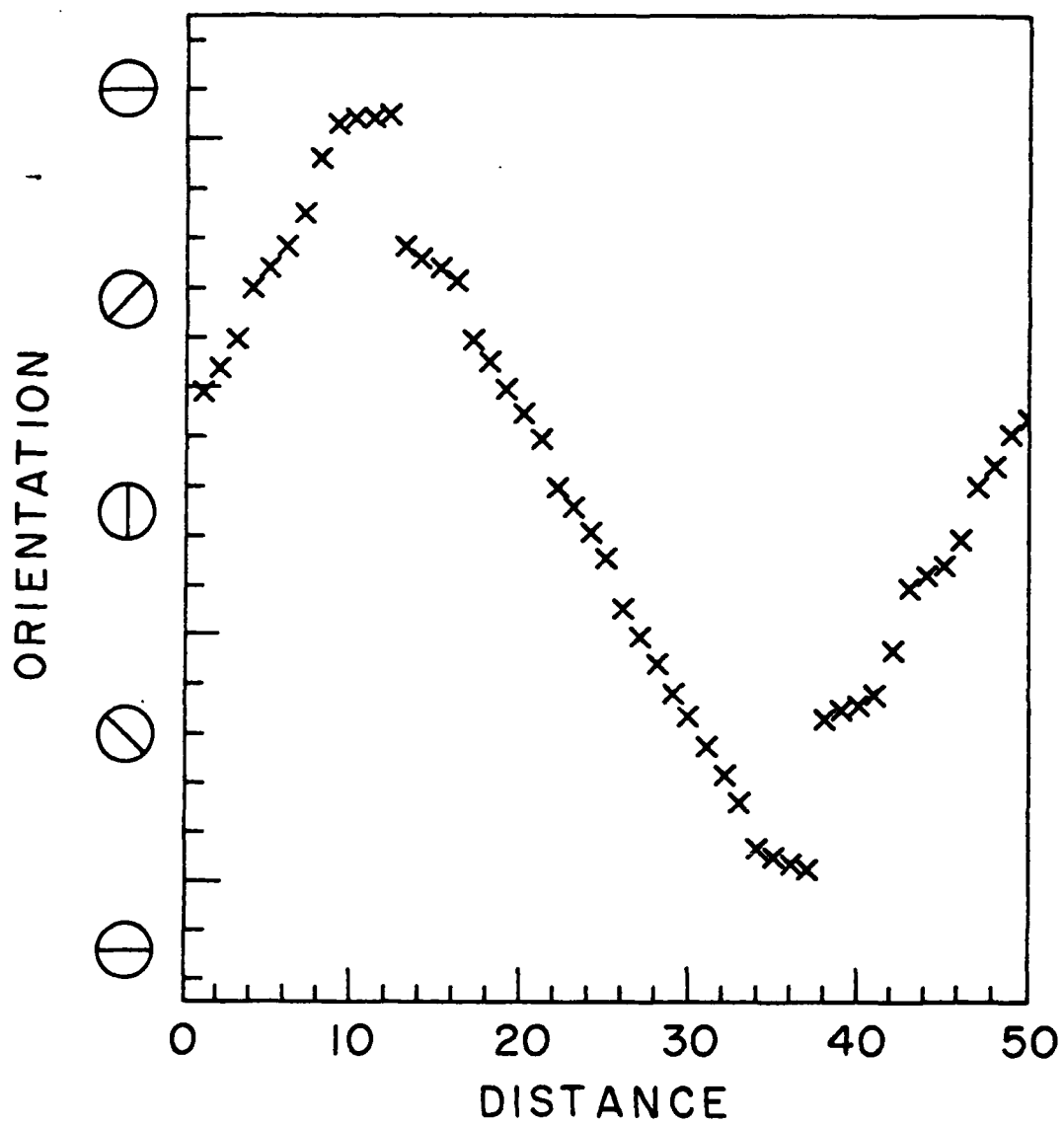


Figure 6.

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